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A new unusual Osteichthyan fish from the Gogo Formation, Western Australia

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Abstract

A unique specimen of a braincase and part of the skeleton of an osteichthyan has been etched from limestone in the Gogo Formation (Frasnian) in the Canning Basin, Western Australia. This has been reconstructed using the standard techniques for interpreting nerves and vascular systems, and an abbreviated reconstruction of the main skeletal features, nerves and vascular structures has been presented. This indicates that the pattern falls outside the range of currently known osteichthyan genera, and we consider that it represents a new pattern of structure evolved from a massive change in the genotype, probably by genomic regulatory systems. Interpretation of the bony skeleton is described using standard observational techniques and serial tomography. The dorsal skull roof consists of a posterior undivided plate with a pointed anterior projection. Ventral to this is another internal support plate attached to the dorsal plate posteriorly and laterally, and medially by vertical stubs. Orbits occur in dorso-anterior position. Strong median ridge ventrally runs anteriorly, and it joins an internasal cartilage. Antero-lateral to the braincase is a large cavity thought to be filled with cartilage in life, and lateral to that and separated from it by a bony sheet, is another cartilage filled space. All these skeletal features are diagnostic of the character of a new group of organisms.

Keywords: Devonian, dermal structure, braincase, cranial nerves, genomic regulatory systems, Osteichthyan patterns.

Introduction

This specimen was found in the Kimberley Region, Western Australia, in the Frasnian Gogo Formation (Fig. 1). The specimen was encased in a small nodule of limestone, and it was etched in acetic acid to expose the remaining bone. The eroded specimen has lost some of the dermal plates, but a well preserved the supraorbital plate and two plates adjacent to it were found in the same nodule. No lower jaw was preserved. The etching has partly destroyed much of the fine bone structure, particularly the thin layers of perichondral bone. Tomography has enabled us to reconstruct some of the missing bone, and we can observe some of the otherwise concealed endocranial bones.

The point in describing this incomplete specimen is that it is so different from other known osteichthyan genera and that it represents a new kind of biological organization in the Devonian, a Period when new osteichthyan patterns were abundant. We have previously described the importance of genomic regulation in the development of new organizations (Campbell & Barwick 2006), and this material is another example of new patterns illustrating the main point of that paper.

Only one incomplete specimen of this form has been found, among the hundreds of etched specimens from this locality. Further searches by ourselves and by other palaeontologists have failed to discover even fragments of the surface ornament. The outstanding state of preservation of the Gogo material, and the failure to discover comparable species elsewhere, indicates that it is a rare species and probably had a limited time and geographical range of occurrence.

We have reconstructed the pattern of some the nervous and vascular systems of the specimens and have represented this incomplete outline without the skeleton. In order to locate these structures for the reader we have indicated the position of some foramina through which the canals pass (Fig. 2). In doing this we have indicated the main factors in our orientation of the specimen. Of course this orientation may be criticised, but the observations of the specimen have to be interpreted in acceptable biological terms. For example, it would be difficult to consider this structure as an eroded braincase of a dipnoan in the light of structures described below.

Orientation of Specimen

In the absence of the pattern of dermal bones, endocranial structures have been the bases for orienting the organism. The lateral walls of the neurocranium are present on both sides of the specimen, and these enclose the braincase in the axis of the structure. We determine the posterior of the specimen because it has the outline of a braincase preserved in thin bone running internally, and having openings into the braincase from the external wall of the neurocranium. What is more there is no sign of a braincase at the anterior of the specimen as we

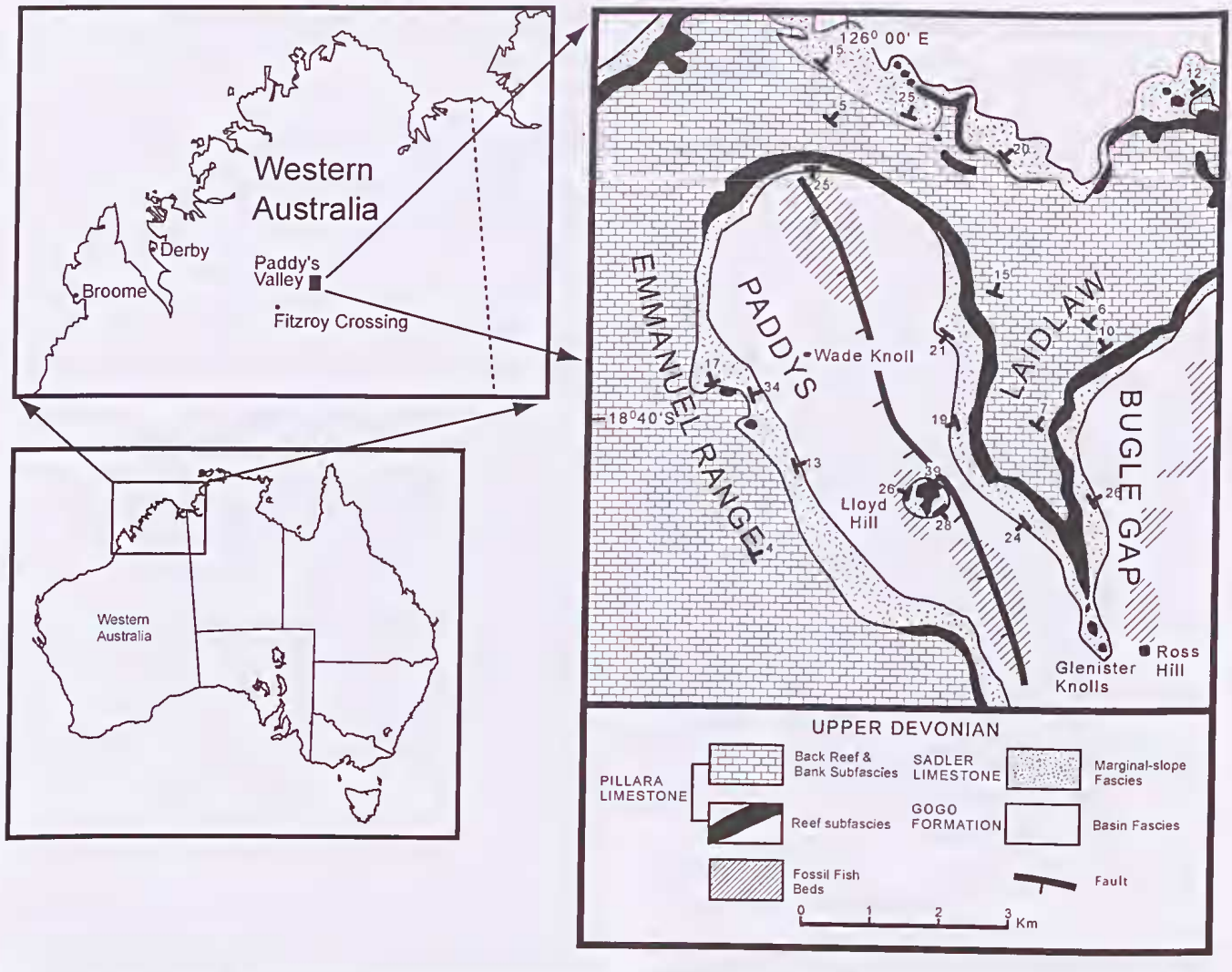


Figure 1. Map showing the position of the Gogo Formation in Western Australia, and the site of the collecting locality. Diagram modified from Andrews *et al*, 2006.

would expected if the specimen were oriented in the reverse direction to what we have proposed. Given this orientation the braincase must be dorsal to the attachment of the notochord, but the specimen is strongly weathered ventral to the braincase and the notochordal attachment has been lost. This orientation indicates not only the posterior end of the specimen but also the dorsal/ventral sides.

The neurocranial walls on each side form relatively robust structures that run almost the length of the specimen. At its posterior end it is eroded and what we consider to have been the lateral commissure has been lost, together with the articulation of the mandible. This would have been a final guide to the orientation had they been present.

This orientation of the specimen also provides the opportunity to recognize the cranial nerves N VIII, N VII, N V and N II in their correct positions. Also although not observed on the external surface, tomography shows the nerves N IX running from the posterior of the braincase in the appropriate position.

Anterior to what we determine as the nerve N VII is a large lateral extension of the neurocranium that houses the largest foramen in the wall (Figs 7, 12, 27). This foramen enters a canal that runs within the neurocranial wall into a branching system of canals that do NOT join the braincase, and must be part of the vascular system. Entering the foramen from a posterior position are two grooves that would have been for the jugular vein and the orbital artery. The size and shape of the foramen and the position of the canals, supports the orientation of the organism as suggested.

Near the proposed anterior end of the preserved specimen there is a gap for the orbit (Fig. 3) and a space for the olfactory capsule (Fig. 14). Running towards the nasal capsule are perichondrally lined tubes that divide anteriorly and terminate in the olfactory capsule or in the lateral walls of the neurocranium (Figs 14, 23). All the above features confirm the complete orientation of the specimen as we have described it below.

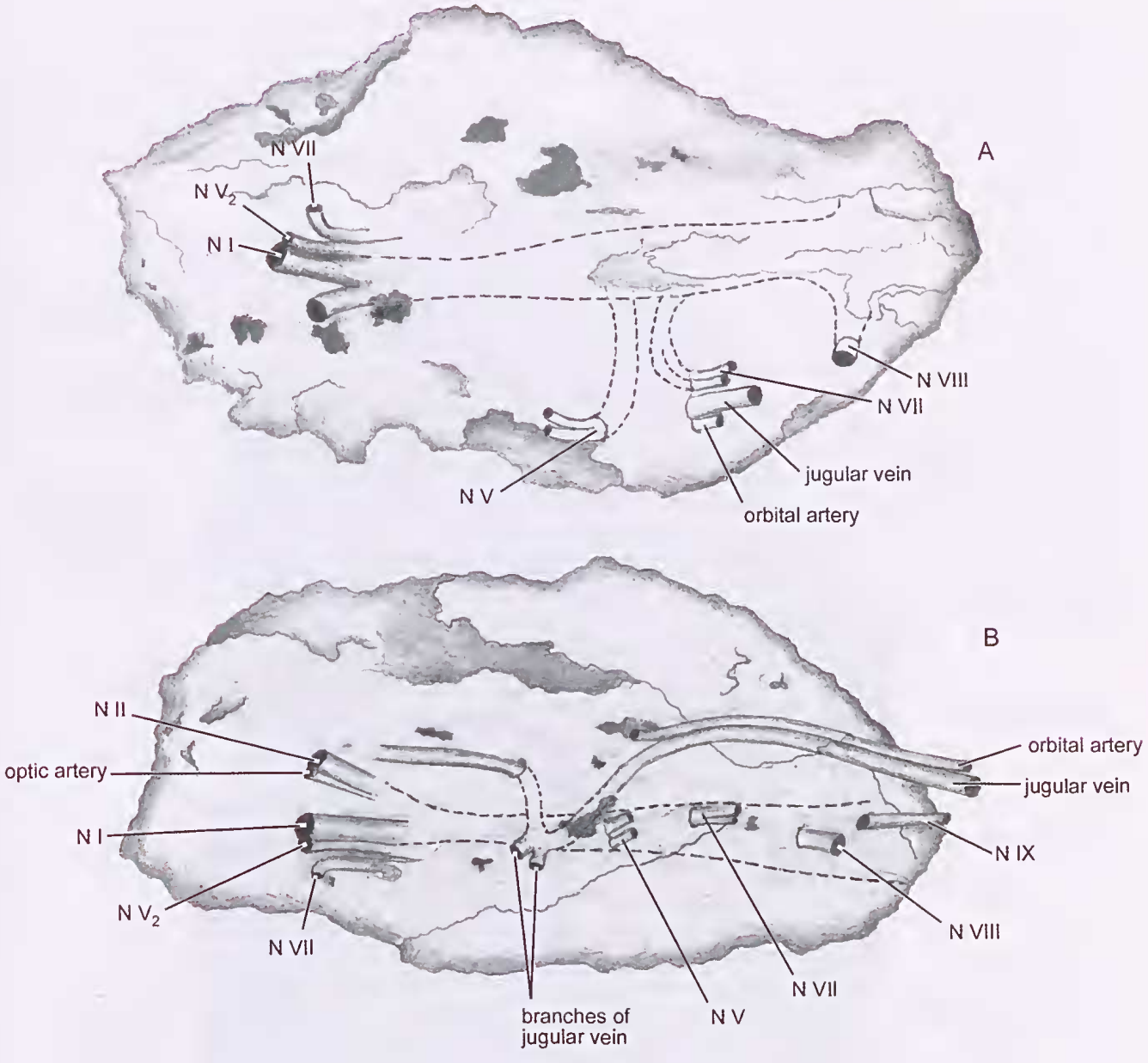


Figure 2. Partial reconstruction diagrams of the braincase of the specimens showing positions of the position of the main nerves and the jugular veins . These give the main position of these structures as a guide to the details set out in the descriptions below. (A) A ventral view of the outline of the specimen with the braincase slightly darkened and the outline of the ossified wall shown as a dotted line. Nerves N V and N VII shown as paired structures because each emerges through two foramina on the specimen. (B) Reconstructed lateral view of the specimen with the braincase slightly darkened. Dotted lines showing jugular vein and the orbital artery from impressions on the neurocranial wall, and the internal course of the jugular outlined from tomography. The internal course of the orbital artery not shown. Course of the optic nerve outlined from tomography but the internal course of the optic artery not shown. Only the left olfactory nerve shown.

Terminology

sub-dermal plate: Large posterior dermal coarse textured plate with thin covering of fine textured bone;

plate 11: Similar to sub-dermal plate separated from it by a strong suture;

internal support plate: Large plate beneath the sub-dermal plate that it joins posteriorly and laterally, but is joined to it medially and anteriorly by bony struts;

triangular plate: Median dorsal plate with triangular outline and carrying small struts, bearing a thin covering plate that was removed during preparation;

centro-lateral cartilaginous space: Open space lateral to the braincase thought to be filled with cartilage in life, but carrying veins and orbital arteries; and

lateral cartilaginous space: Smaller open space lateral to the median cartilaginous space and separated from it by a neurocranial wall, and carrying veins and orbital arteries.

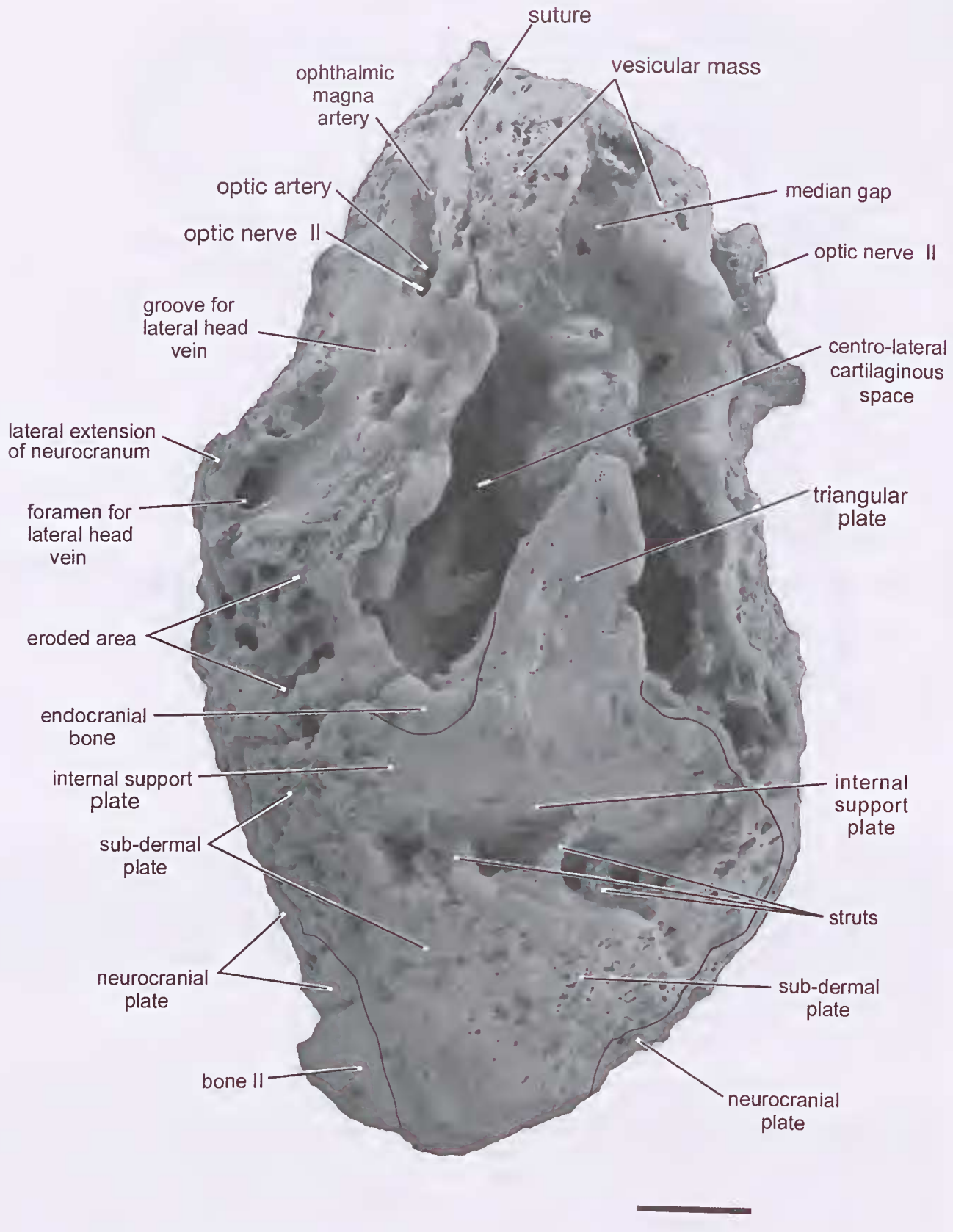


Figure 3. Dorsal view of whole specimen illustrating all the major features mentioned in the interpretation in the text. Outline of suture bounding the sub-dermal plate and anteriorly the internal support plate, in a solid inked line. Scale = 10mm.

Systematic Palaeontology

In the absence of a pattern of dermal bones and of a palate, we have been uneasy in assigning a formal taxonomic name to this isolated specimen. However, further reference to the specimen by ourselves and any other authors would find it convenient to have a formal taxonomic name.

Genus *Cainocara* **n.** gen.

Type species: *Cainocara enigma* n, sp.

Etymology: kainos (Gr) new: kara (Gr) head: enigma (L) obscure

Type specimen: ANU 46543 from Paddy's Valley, Gogo Formation, Western Australia.

Location of specimen: ANU = Australian National University.

Description:

Postero-dorsal surface: The exterior of the skull roof is not preserved, but the surface of the specimen is made of a sub-dermal plate (Fig. 3). This plate has patches of very fine grained bone on its surface, and this is bound into the underlying coarse bone (Fig. 12B). This fine bone we regard as the preserved remains of the original dermal surface. The suggestion that the sub-dermal plate is endocranium is not supported by the specimen. A lateral extension of the neurocranial bone curves anteriorly towards the triangular plate (Figs 3, 4). The triangular plate as is shown on Figures 24, 25, is made of the internal support plate (see below), and this implies that a layer of the sub-dermal plate originally covered the internal support plate on the triangular plate. This extends anteriorly beyond the mid-length of the specimen; the anterior end of the plate was lost during preparation.

Ventral to this large sub-dermal plate is the internal support plate (Figs 5, 6) that meets the triangular plate anteriorly at an angle of ca. 20°. The triangular plate is shown by tomography to be an extension of the internal support plate. Tomography illustrates that a canal runs ventrally off the triangular plate in a posterolateral direction (Figs 4, 25), and it seems to open into the large internal space that forms the edge of the perichondral inner lining of the centro-lateral cartilaginous space. Posteriorly and laterally the internal support plate joins the sub-dermal plate. As shown on Figure 5B, the internal

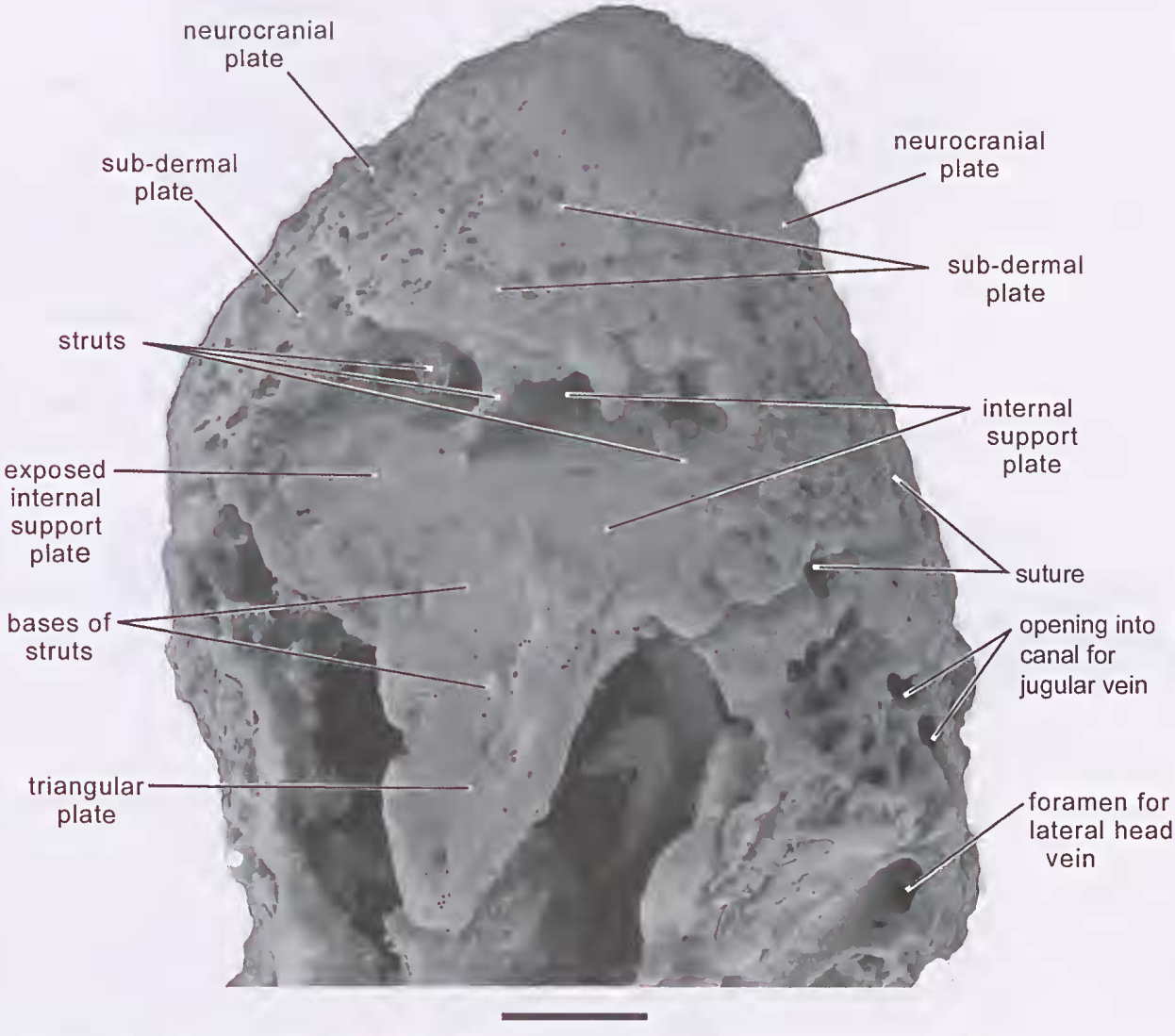


Figure 4. Slightly tilted and slightly modified dorsal view of posterior of specimen showing details of the dorsal structures more clearly than on Figure 3. Foramen in triangular plate leading to canal. Scale = 10mm.

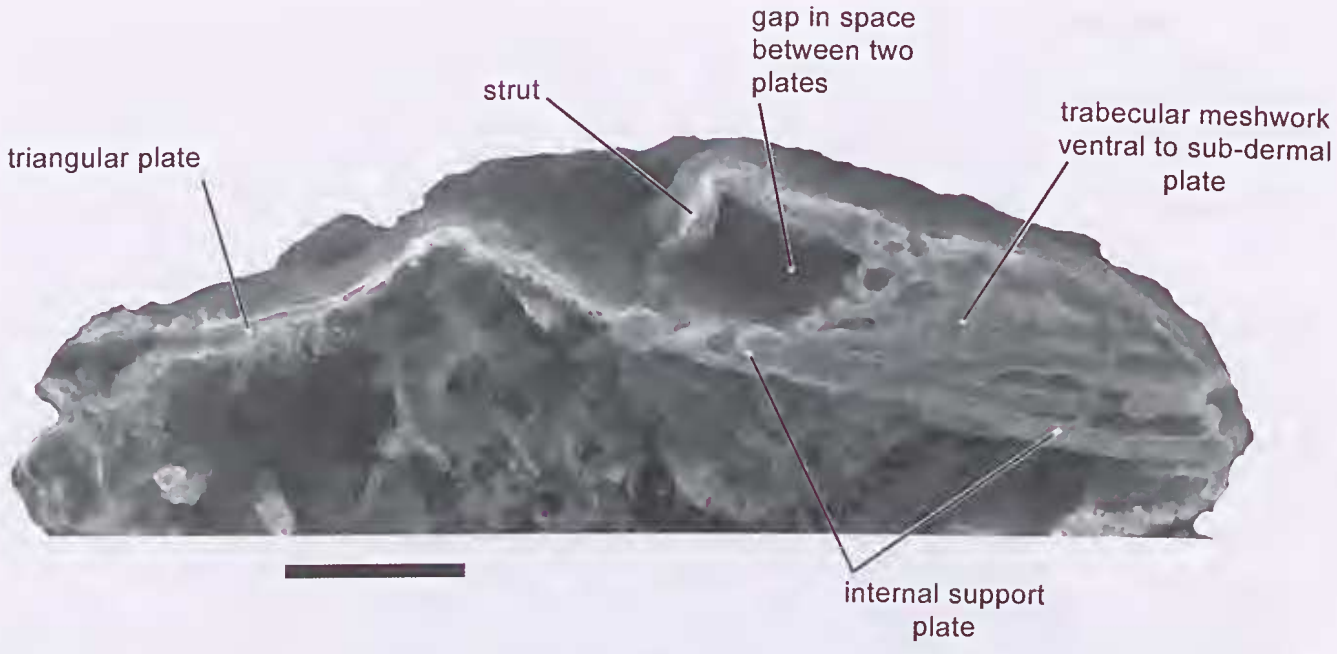


Figure 5. Thick tomographic section through the posterior part of the specimen showing the position of the internal support plate, and its supports to the sub-dermal plate. Scale = 10mm.

support plate continues towards the posterior extremity, but as shown on Figure 7B it does not reach the limits of the specimen. The trabecular meshwork lies directly on the neurocranium.

X-rays show that the internal support plate is made of fine-grained bone easily distinguished from the sub-dermal plate. Posteriorly these two plates are joined by a trabecular meshwork of plates and anteriorly by a series of bony struts (Figs 5, 6B, 13, 24, 25). The braincase lies three or four mm ventral to the internal support plate.

In the posterior view of the specimen the braincase is separated from the neurocranial walls by a small gap that we interpret as occupied by cartilage (Fig. 6A). This also would have occupied the space around the lateral and ventral parts of the bones. The walls of the braincase are preserved as a thin layer of bone. The posterior extremity of the braincase is not preserved, but the position of the neurocranial walls indicate that only a small amount of the braincase is missing. The thickness of the posterior part of the braincase indicates that it carried the dorsal paired canals described below.

The posterior of the specimen (Fig. 7A) has a fragment of another dermal plate labelled bone II. Its surface is also made of the fine grained bone such as occurs in patches on the sub-dermal plate, and its base in made of a layer of coarse bone. It is part of the dermal skeleton, and details of its surface are shown on Figure 12B. Two posteriorly-viewed images of tomographic sections (Figs 7B, C) through the posterior of the specimen and through the jugular foramen are significant. The internal support plate (Fig. 7B) lies directly on the neurocranial bone, and the trabecular network filling the internal space. Figure 7C is a section through the jugular foramina the right side retains some of the internal structure that will be dealt with in a subsequent section.

Bones of the Circumorbital Fragment

This section describes the only isolated dermal bone preserved, and it was found with the skeleton in the limestone nodule. It has the edge of the orbit preserved (Fig. 8B) and attached to it are two other dermal bones that have not been identified. The orbital fragment has no lateral line and it is therefore not an infraorbital. Being a supraorbital we have assumed that the pattern of ornament on these and the adjacent bones represents the pattern of ornament of the skull roof.

One end of the supraorbital plate thickens considerably, but the other end has lost some of the internal bone. Cross section of the thicker bone (Fig. 8A) shows three distinct layers: (a) the outer layer has about the same or slightly greater thickness as the inner layer, and it is composed finely perforated bone. No large trabecules like those of the median layer are present. Surface bosses range from 0.2 mm to 1.2 mm in diameter. Sections of the bosses show that they range in height from 50–200μ; (b) the median layer is much thicker and consists of trabecular bone. Its contact with the inner layer is clear. Thin sections show large osteocytes. In addition to the osteocyte spaces there are linear slits (Fig. 8A) that suggest the presence of blood vessels; and (c) the inner layer is of fine porous grained bones.

The structure of the external bosses is best examined in direct images from the exterior, especially in bosses that have been just forming or are partly resorbed (Fig. 10 B). As shown on Figures 8C, 10A, B, the bosses overlap the outer layer of the bone. Bosses are composed of several sheets of superimposed layers. Perforations, as shown on Figure 9B, are common, but other layers are less perforate. Apparently each layer of the boss contains both types of tissue. As shown in Figs 8C, 9B, 10B, these layers are not continuous over the whole surface of the boss, but occur in patches. Fig. 9B shows the upper layers of

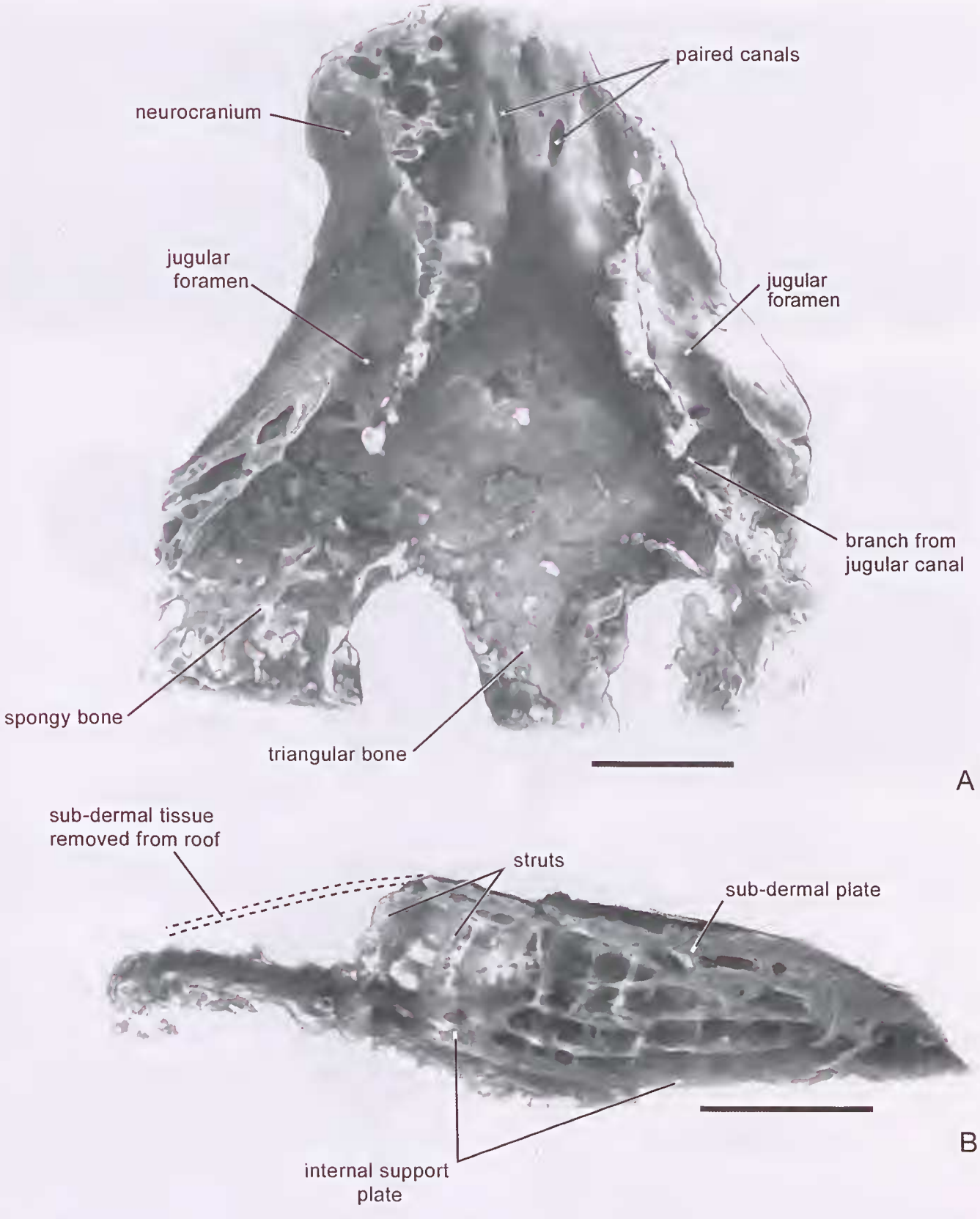


Figure 6. A. Dorsal view of a thick tomographic image of an oblique section cut dorsal to the braincase posteriorly, through the jugular vein, and the triangular plate anteriorly. Dorsal part of the organism removed. A pair of canals reach the posterior edge of the specimen. They must arise from the top of the braincase which lies ventral to this section. They could be for endolymphatic ducts or alternately nerve N X. Neurocranial bone shown posteriorly and anteriorly as spongy bone. B. A thick tomographic section through the posterior part of the specimen with the sub-dermal plate lying on the coarse bony tissue. Posterior part of the internal support plate missing. Anteriorly the subdermal plate was removed during preparation, and its position on the diagram is shown by dotted lines. The area marked as struts also shows the thickening of the bone on the other side of the specimen (see also Fig .5). Scale = 10mm.

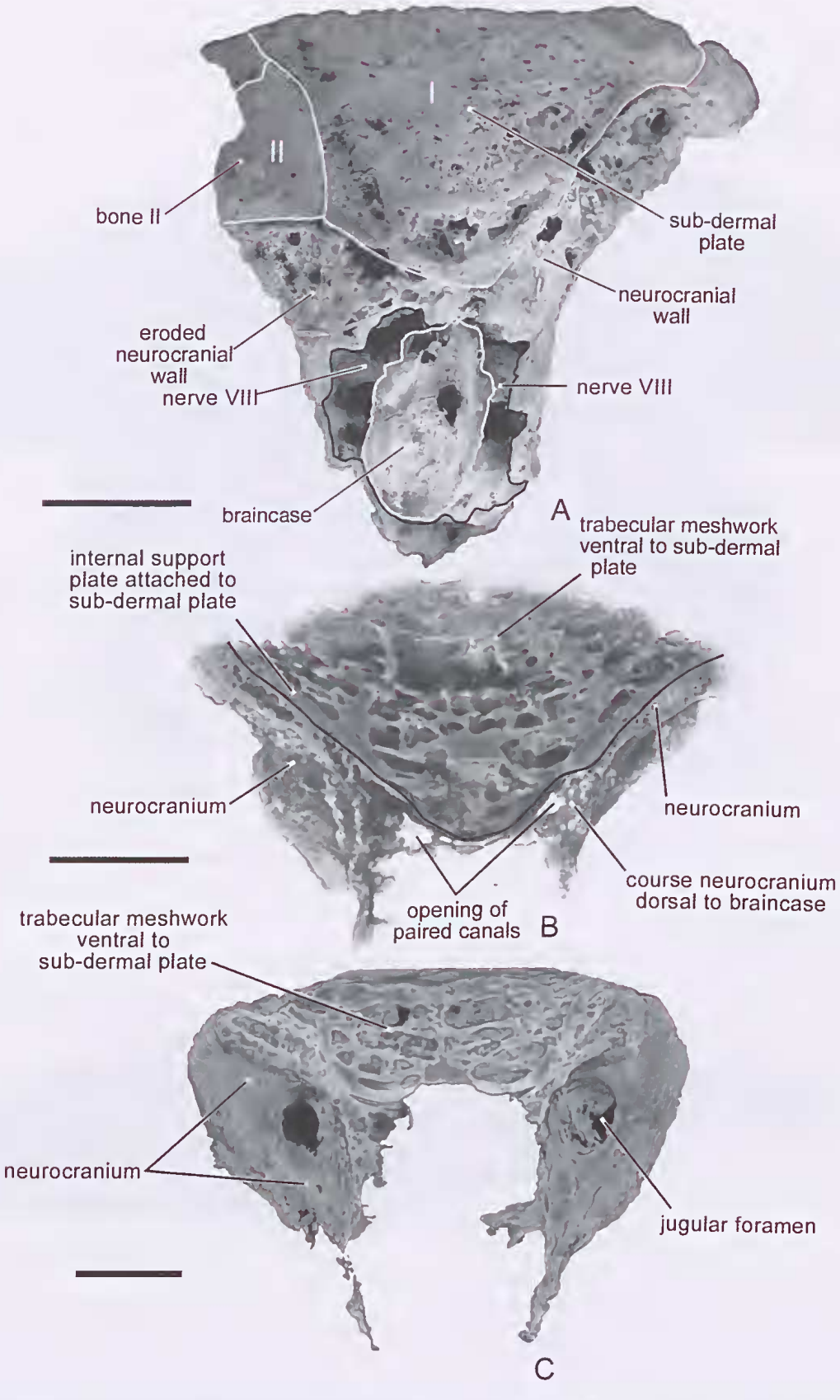


Figure 7. A. Modified image of photograph of posterior of specimen. Right side of specimen more deeply eroded than the left. Sutures bounding the sub-dermal plate, and the neurocranial wall are outlined by a white line. Space around the braincase wall left for cartilaginous material left blank. Canals carrying nerve N VIII present on the two sides. B. Thick tomographic image of a continuous section across the posterior part of the specimen, showing the internal support plate attached to the neurocranial wall but posteriorly disappearing. Suture bounding the neurocranial plate emphasised by a blackened line. Trabecular meshwork between the internal support plate and the sub-dermal plate clear, but exposing a large median gap. C Transverse thick topographic image of continuous section taken posterior to the jugular foramen, and therefore anterior to image in Fig B. Scale = 10mm.

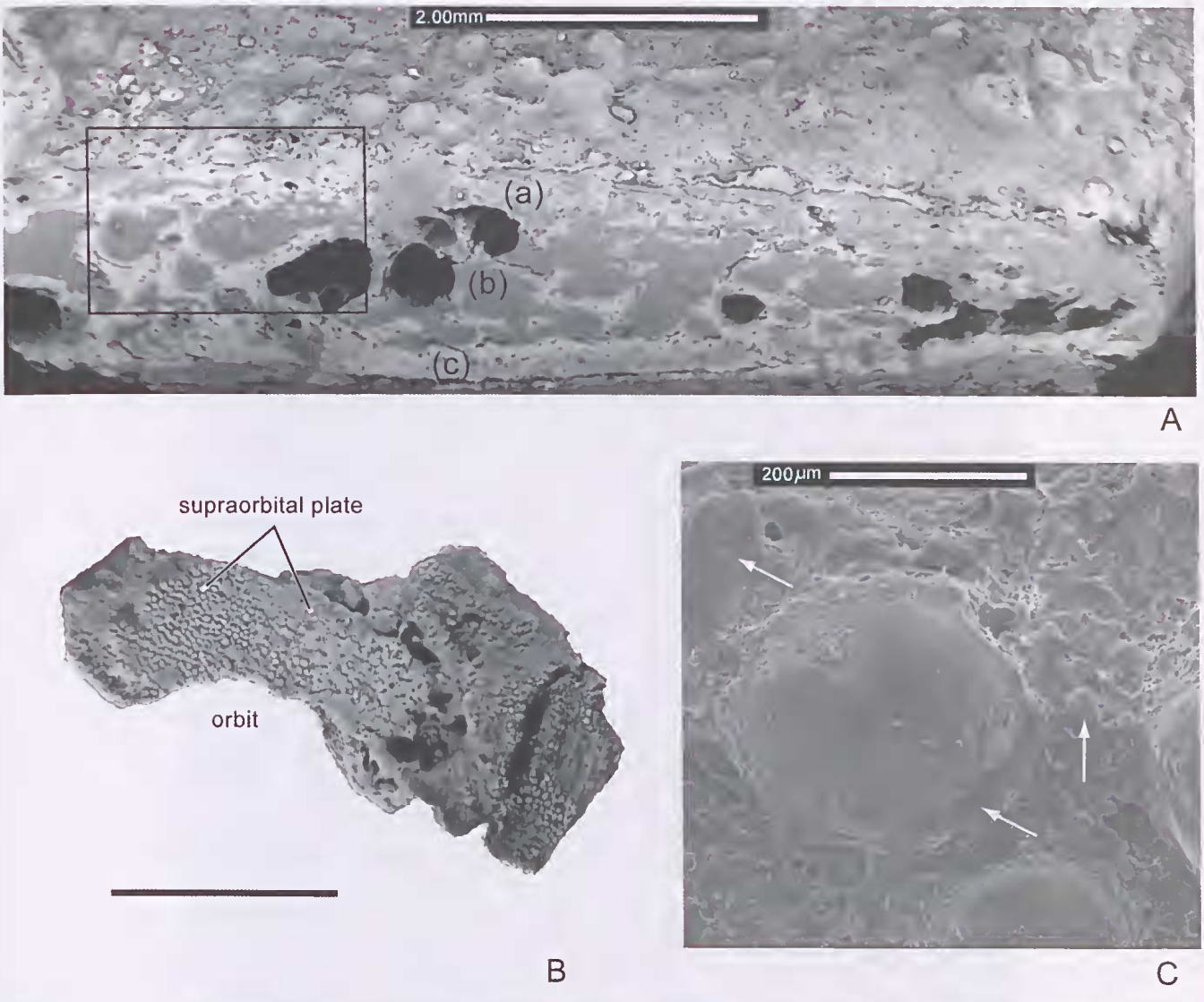


Figure 8. A. Cross section of the bone adjacent to the supraorbital plate as shown in Fig. 8 B. Top surface with the bosses still in position. The outer layer shown by (a); the coarse middle layer by (b); and the inner layer by (c). B. The isolated fragment of the supraorbital bone and the surrounding bones. Bosses on the surface similar on all plates. C. An isolated boss showing the areas between the bosses largely overlapped by layers developed from the first layers of tissue forming the boss (white arrows). Basal bone. largely obscured. Scales as shown.

bone with outgrowing edges. As shown in Fig. 10B where a boss has been partially destroyed, up to 7 numbered layers of sheets form a sequence. This kind of structure has not been observed previously in any osteichthyans.

Elsewhere the surface has a continuous layer of tissue of boss-like tissue (Fig. 11A). As has been shown above (Fig. 11B), the margins of some layers cover the bones between the isolated bosses. In some places there is even connection between the layers of tissue between the bosses (Fig. 11A). The interpretation of these structures remains problematic.

The mode of deposition of the layers on the tubercles is significant. The first deposited layers are those at the base of the boss and these must continue to expand during the growth of the animal. Note that it is these early layers that are the most extensive. Subsequent layers are deposited on these early layers and are progressively more restricted. Their margins would have been covered with epidermal tissue and so their margins would have continued to grow. This is shown on the enlarged margin on Figure 9B in which the growing edges of the layers were exposed.

So far as we are aware, this kind of depositional pattern is not known in any known primitive fish.

Endocranial Structures

The neurocranium wall consists of a single unit, and tomographic sections show that it is made of moderately thick bone. These two pieces of evidence are vital in understanding the assignment to a higher group. The neurocranial walls are extensive on the left side of the specimen, but they were lost anteriorly on the right side by erosion.

Lateral Walls of the Neurocranium: There is a large space between the outline of the braincase and the neurocranium. In Early Devonian dipnoans this gap is

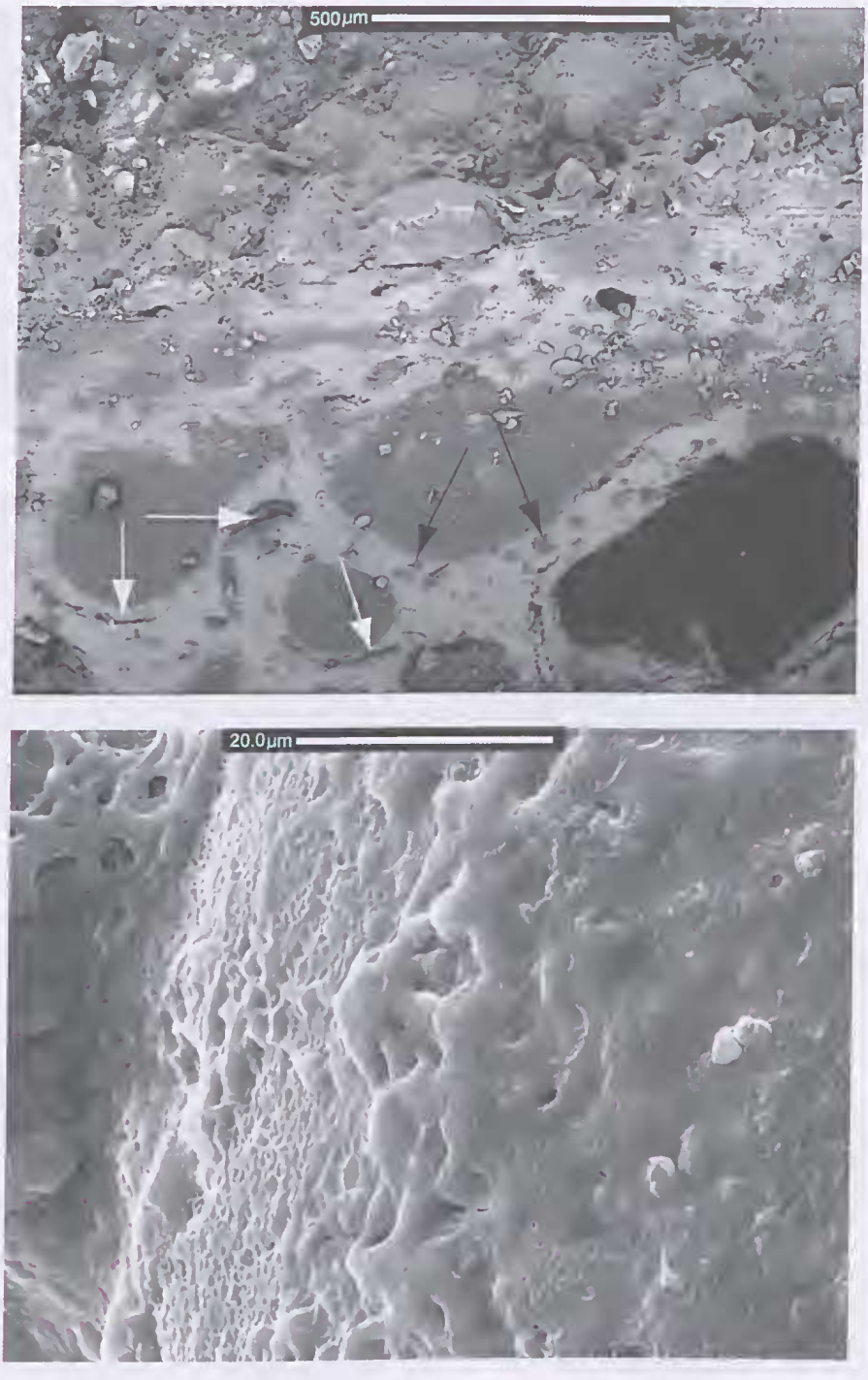


Figure 9. A. An enlargement of the area marked on Fig. 8 A. Bosses shown at top of figure. Osteocyte spaces (black arrows) in bone around the open spaces. Small slit like spaces (white arrows) possibly indicating blood vessels. B. Enlarged margin of a boss showing the edges of the superimposed layers and the basal bone on left side of image. Note the very fine pores in the most superficial layer and pores in the margins of the deeper layers. Scales as shown.

very narrow, but *Chirodipterus* from the Late Devonian has a much larger gap.

On each side of the specimen is a foramen that is up to 3.5 mm in diameter, and passes through the neurocranial walls and enters the braincase via ossified canals. The size and position of the foramen and its orientation indicates that it had a major function. This suggests that it could have been for the acoustic nerve N VIII leading out to the semi-circular canals. Obviously this implies that the labyrinth space and the semicircular canals were not connected directly into the braincase as is normal for osteichthyans, and this could be a major objection to our proposal that the organism is an osteichthyan. There is no doubt however that the ossification of the walls of the canal from this foramen clearly enters the braincase (see also tomographic sections in Figs 24A, B). The position of nerve N IX is now interpreted as running posteriorly to the edge of the specimen (Figs 12, 25B).

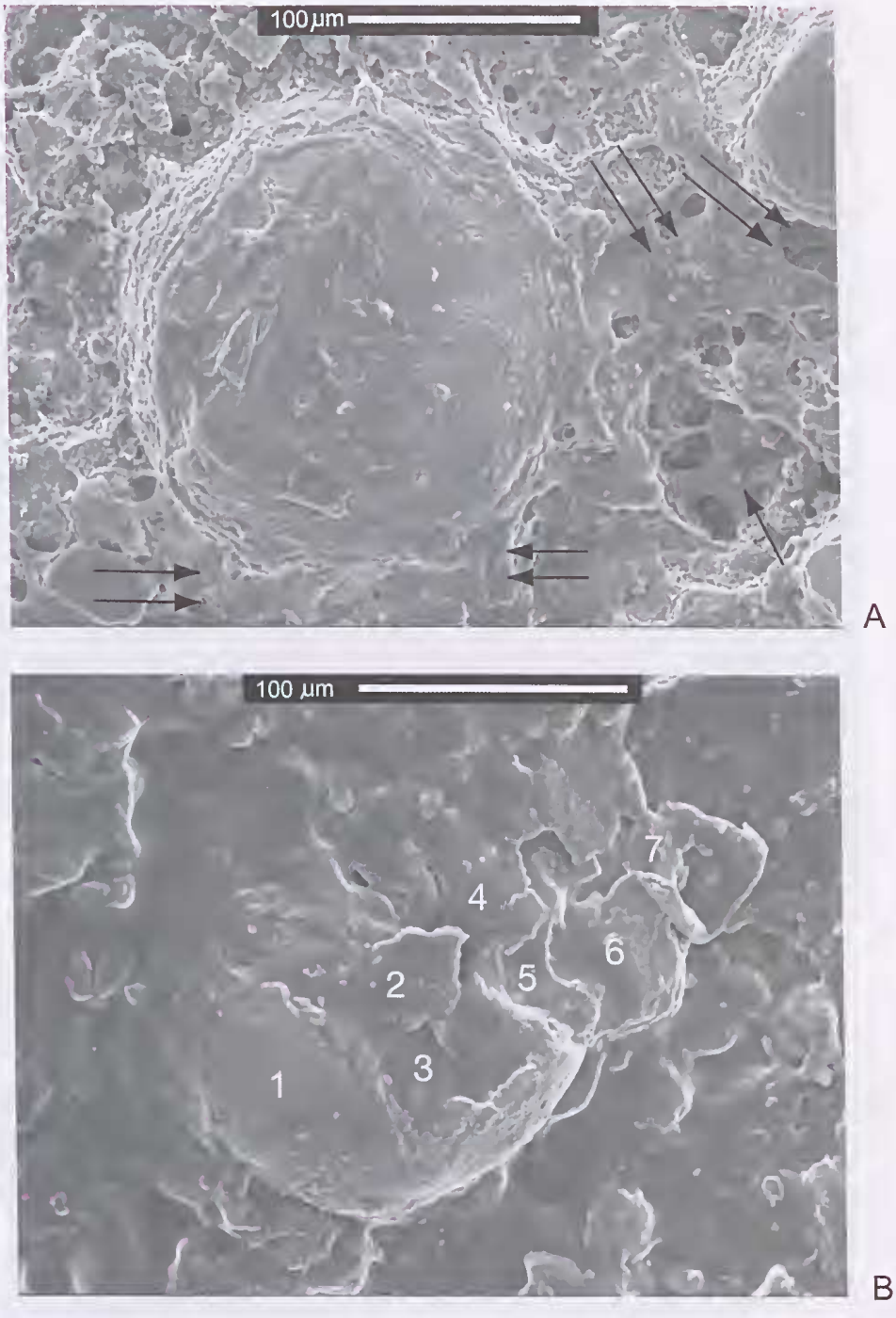


Figure 10. A. Isolated boss showing the incomplete layers on the surface, successive deeper layers, the more widespread lower layers with double arrows indicating the extensive basal layer, and a single arrow at the exposed basal bone layer. B. An isolated boss that was partly destroyed and shows the superimposed layers 1–7. The sequence interpreted from overlaps. Scales as shown.

Tomographic section in Figure 6A, as well as showing the jugular veins in section also shows a pair of canals running posteriorly. These must originate from the top of the braincase as shown in the explanation of the figure, and they run to the posterior edge of the specimen (Fig. 7B). These may be for ductus endolymphaticus or alternately for nerve N X. For the present we give them the labels "paired canals". On each side of the specimen, 15mm anterior to nerve N VIII, the neurocranial wall contains an oval depression in the floor of which are two foramina. The grooves run internally in an antero-ventral direction from these foramina and we conclude that they enter the braincase (see tomographic section 25A, B). In living vertebrates the facial nerve N VII leaves the braincase to form the hyomandibular, palatine and buccal nerves. In our specimen, these two foramina open in a postero-lateral direction and are appropriately placed to contain branches of nerve N VII (Fig. 12A).

The surface of the specimen dorsal to nerve N VII there are small foramina that are difficult to trace internally but they do not appear on the tomographic sections as entering the braincase. We interpret them as nutrient foramina.

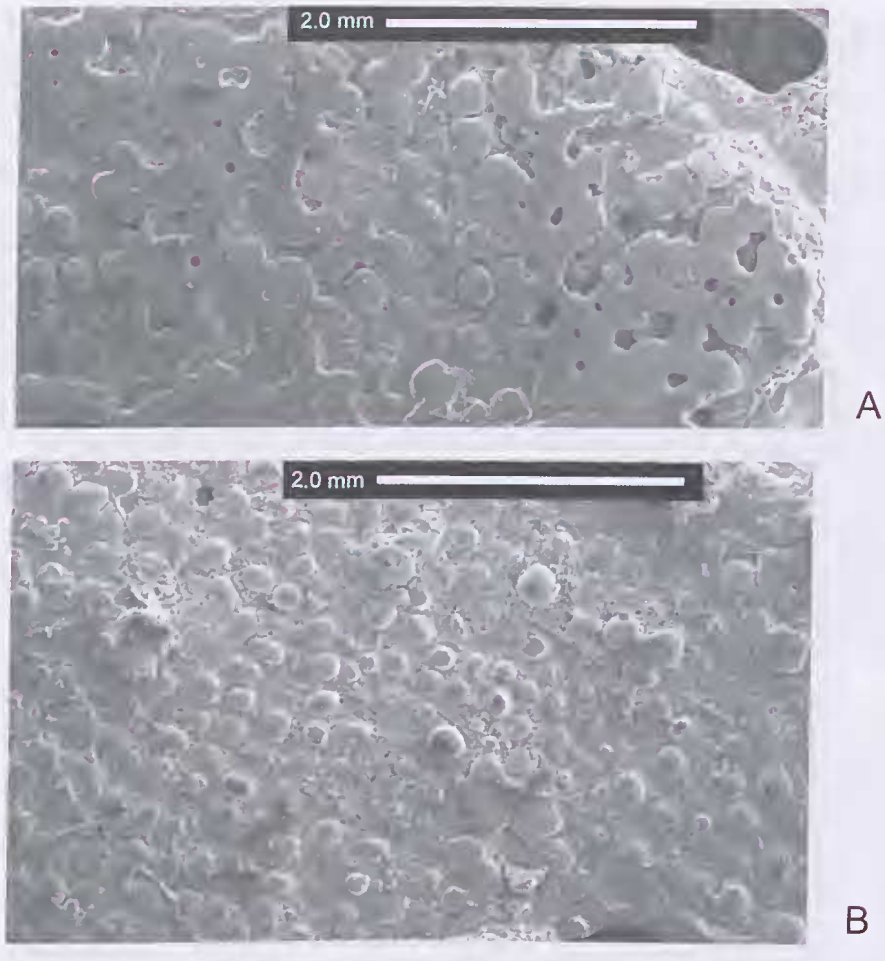


Figure 11. A and B. Two views of the surface area on the supraorbital plate. A. Has the bosses joined. B. Has the bosses separated. Scales as shown.

Dorsal to the foramen for nerve N VII, the neurocranial wall forms an even surface, and dorsally it turns laterally and runs anterolateral for 25mm to form a lateral process (Fig. 2). This is a larger and more posterior extension of the neurocranial wall than is found in any other osteichthyan. At the posterior end of this lateral extension is the largest foramen in the neurocranial wall shown on (Figs 6A, 7C, 12A and tomographically on Fig. 24A). Two shallow grooves in the neurocranial wall enter this foramen from the posterior direction. On the dorsal side is a smooth surface that runs into the foramen (the orbital artery), and on the ventral side is a larger groove within which are tiny openings that enter the wall (the jugular vein). This latter groove can be traced posteriorly for a short distance where it apparently turns laterally. Presumably these two canals enter the preserved specimen from a postero-ventral position, having entered the region through the bone that forms the unpreserved lateral commissure of the specimen. We have named this large foramen as the 'jugular foramen'. In other Devonian dipnoans the jugular vein runs lateral to the neurocranium, but in this new organism it definitely runs medial to the neurocranium mainly because of the large posterior extension of the neurocranial wall. This is just another difference from dipnoans.

Both the jugular vein and the orbital artery are visible, after entering the large foramen the internal walls of (Fig. 24 A). Both canals turn laterally, and the jugular turns towards the lateral neurocranial process. Its course can be followed tomographically (Fig. 26A, B). It forms a large U-shaped outline, and it passes anteriorly into a foramen 3mm wide for the lateral head vein (Fig. 26). There its presence can be observed on the specimen, and it bends anteriorly to a large foramen that we interpret as the foramen for the lateral head vein (Fig. 17). A furrow continues anteriorly along the dorsal surface, and this is described below.

Where the jugular canal turns dorso-laterally towards the lateral neurocranial process, a number of foramina open ventrally out of the canal (Fig. 26A), and these open into the Lateral Cartilaginous Space.

Tomography indicates that ventral to the jugular canal; a separate canal runs anteriorly and separates into an isolated canal that passes to the lateral wall of the specimen lateral to the Lateral Cartilaginous Space. This is labelled as the anterior orbital artery (Figs 17, 18, 27B, C). Another large opening lies posterior to lateral neurocranial process (Figs 17, 18). A notch in its anterior edge continues into the neurocranial wall indicating that the canal passes ventrally from it. Posterior to the openings on the dorsal surface an expanding canal runs postero-ventrally towards the jugular foramen (Figs 17, 18), but as this cannot be part of the jugular system, it can only be part of the branch of the posterior orbital artery

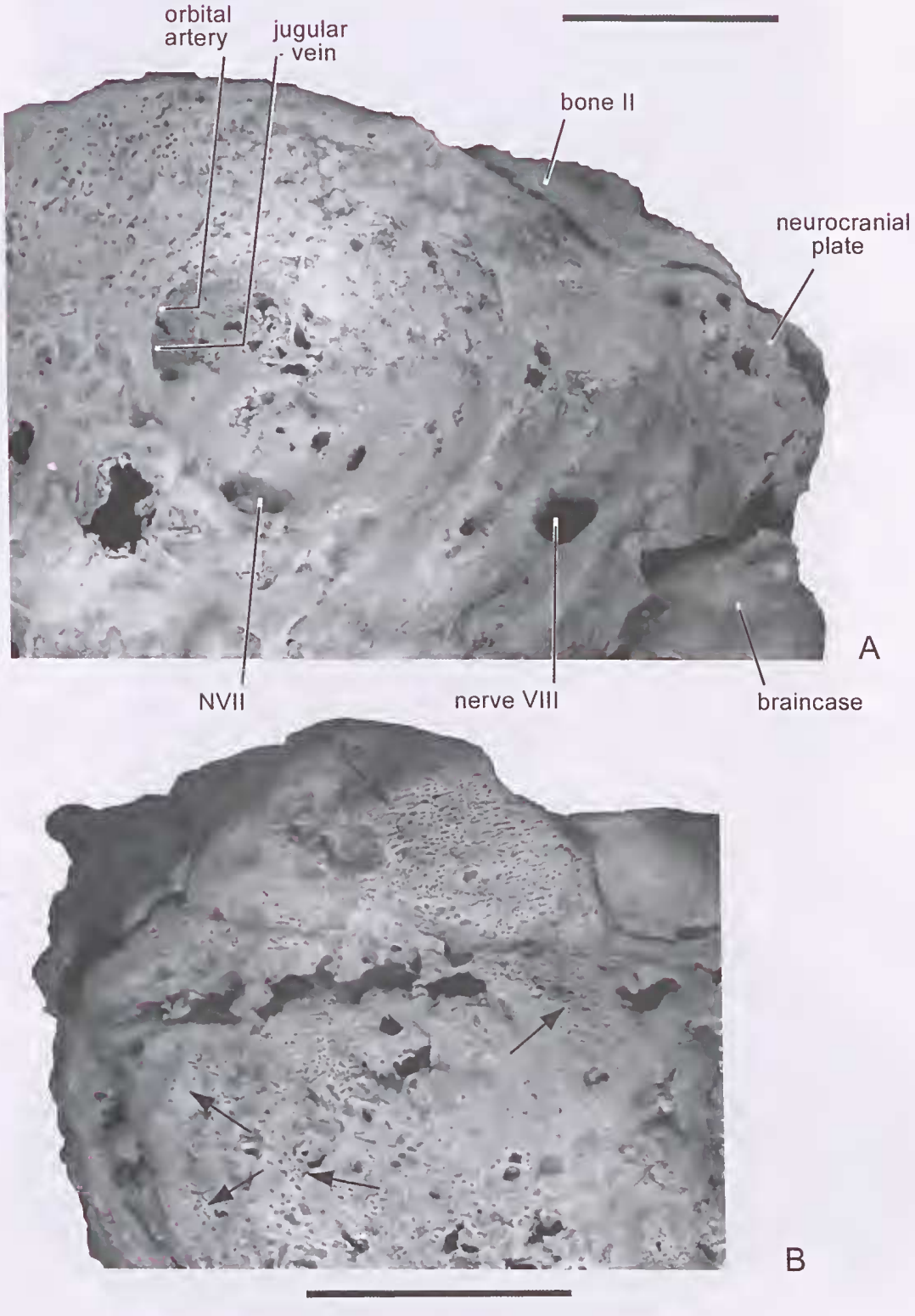


Figure 12. A. Lateral view of the posterior half of the specimen. The large jugular foramen is shown in lateral view, with entrances for the jugular and orbital artery. The latter runs posteriorly in a shallow groove. Foramina for the cranial nerves to the braincase lie in the neurocranial plate. The base of bone II surmounting the eroded neurocranial wall. Nerve N VII is in a depression with two foramina clearly exposed. B. Enlarged dorsal surface, with fine bone on surface of bone II at the top of the figureand on the adjacent surface of subdermal bone (black arrows). Scales = 10mm.

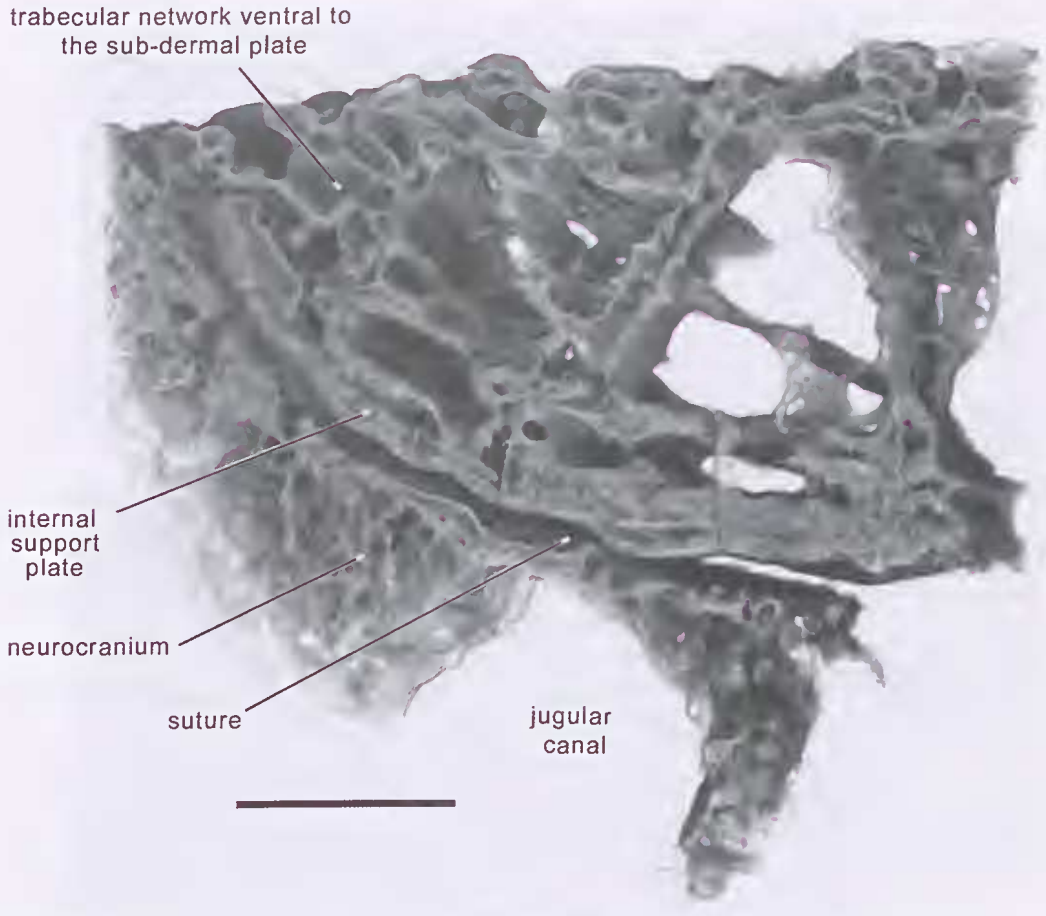


Figure 13. Tomographic image of a thick section cut across the dorsal side and across the roof of the jugular canal. The strong suture between the internal support plate and the neurocranial plate. The coarse tissue and a large gap dorsal to internal support plate. Scale = 10mm.

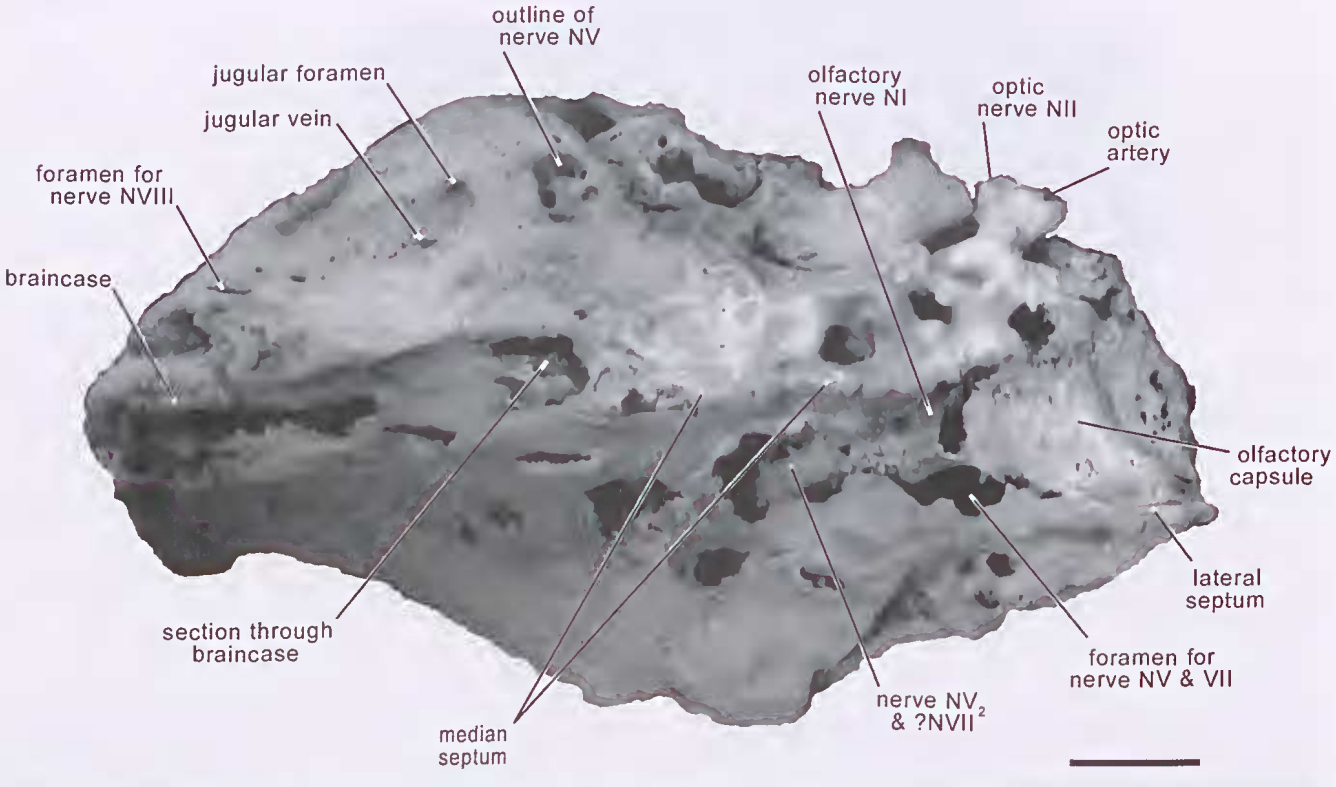


Figure 14. A. Ventral view of whole specimen. Entrance of olfactory nerve to olfactory capsule broken. Dark line across the nasal capsule indicates the anterior edge of the capsule, with the external nostril to the top right. Scale = 10mm.

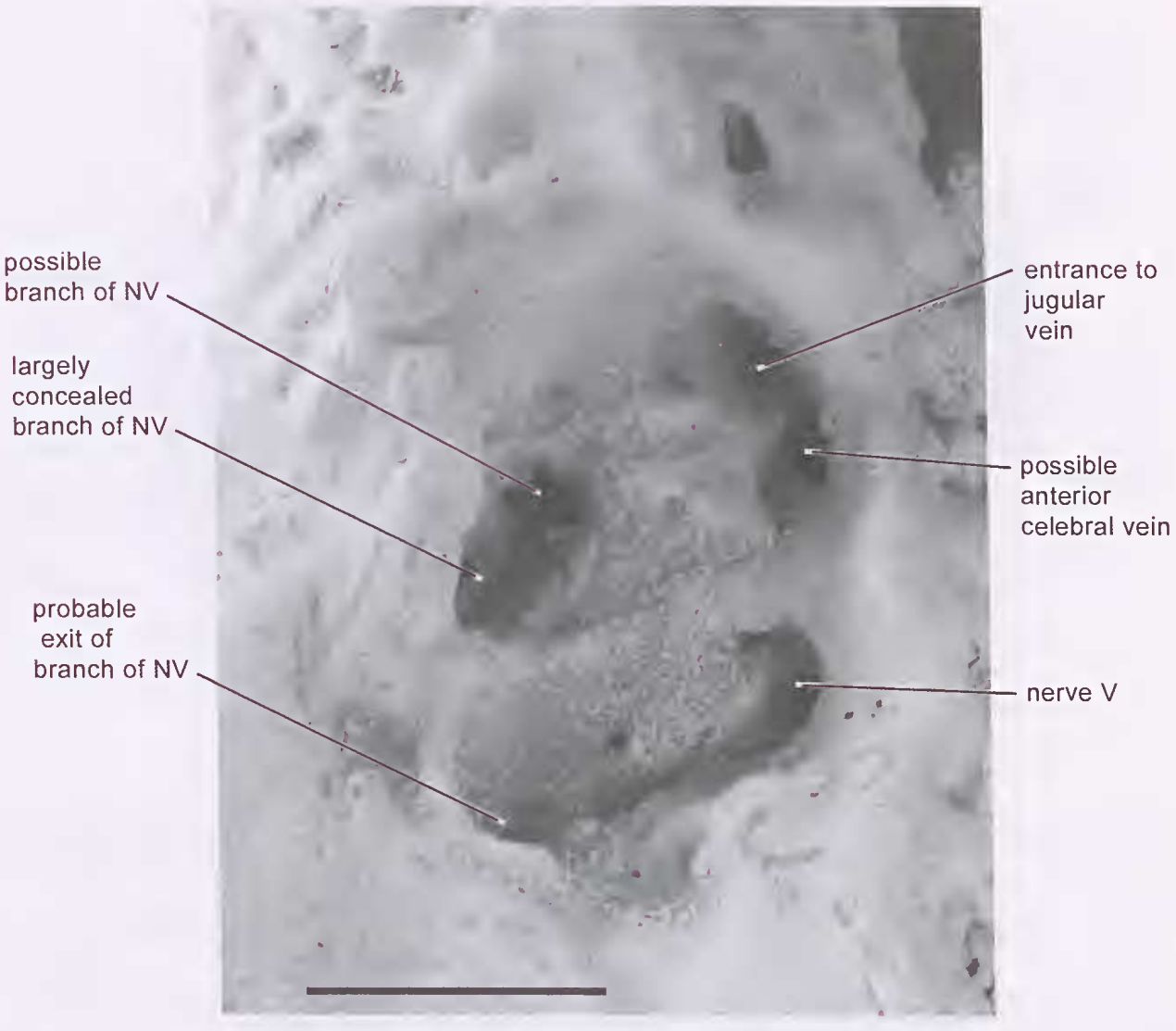


Figure 15. Diagrammatic enlargement of the gap around the space for nerve N V as shown on Fig. 16. The area is surrounded by a rim of bone, and the foramina are placed within this rim. Some of these are emphasised. The two foramina labelled nerve N V (the ventral one partly concealed by the surrounding rim) open into deep canals that run into the braincase. The dorsal of these two canals has a branch labelled possible branch of nerve N V, and it runs dorsally but its function remains unknown. Dorsally a foramen runs to the jugular area, and a lateral branch connected with this foramen is labelled cerebral vein. The bottom right has a foramen labelled nerve N and this may be a trigeminous branch. Scale = 10 mm.

system. Tomography of this area is not clear, but canals inside the jugular foramen open appropriately to permit the orbital artery to pass out in appropriate directions.

On the dorsal surface an eroded area is indicated on Figure 17. Sections indicate that the trabeculae within this space do not make a connected series, and we consider that this mass forms a supporting series of plates.

Anterior to the jugular foramen, the left side of the specimen has a single opening, but the right side has the wall slightly eroded and exposes an intricate structure. In the base of a largely rounded depressed space, is a complex arrangement of foramina for both nerves and veins (Figs 14, 15). On the posterior side there are two foramina each of which is surrounded by a slight ridge. Foramina occur posteriorly, and these run postero-ventrally towards the braincase. Its course as it approaches the braincase is shown on typographical sections (Figs 24A, B). We interpret these as carrying trigeminus nerve N V. Just dorsal to the top foramen for nerve N V is a second foramen that cannot be traced internally. It is labelled on Figure 15 as another branch of nerve N V. At the dorsal extremity of the large depression is a foramen that opens dorsally for a connection with the jugular vein. Just ventral to that foramen is a second foramen the runs anteriorly into the centro-lateral cartilaginous space. We interpret this as carrying a vein, possibly the anterior cerebral vein (Fig. 15). At the anterior edge of the main depression is another foramen that runs antero-ventrally into the broken area around the cartilaginous space. Posteriorly this foramen is by a furrow to the ventral foramen previously identified as for the nerve N V. Therefore we consider that a branch of trigeminous nerve N V passes into the centro-lateral cartilaginous space. Details of this structure are shown diagrammatically drawn from photographs (Fig. 15), but with some of the foramina emphasised because they were covered with the raised rim around the whole structure.

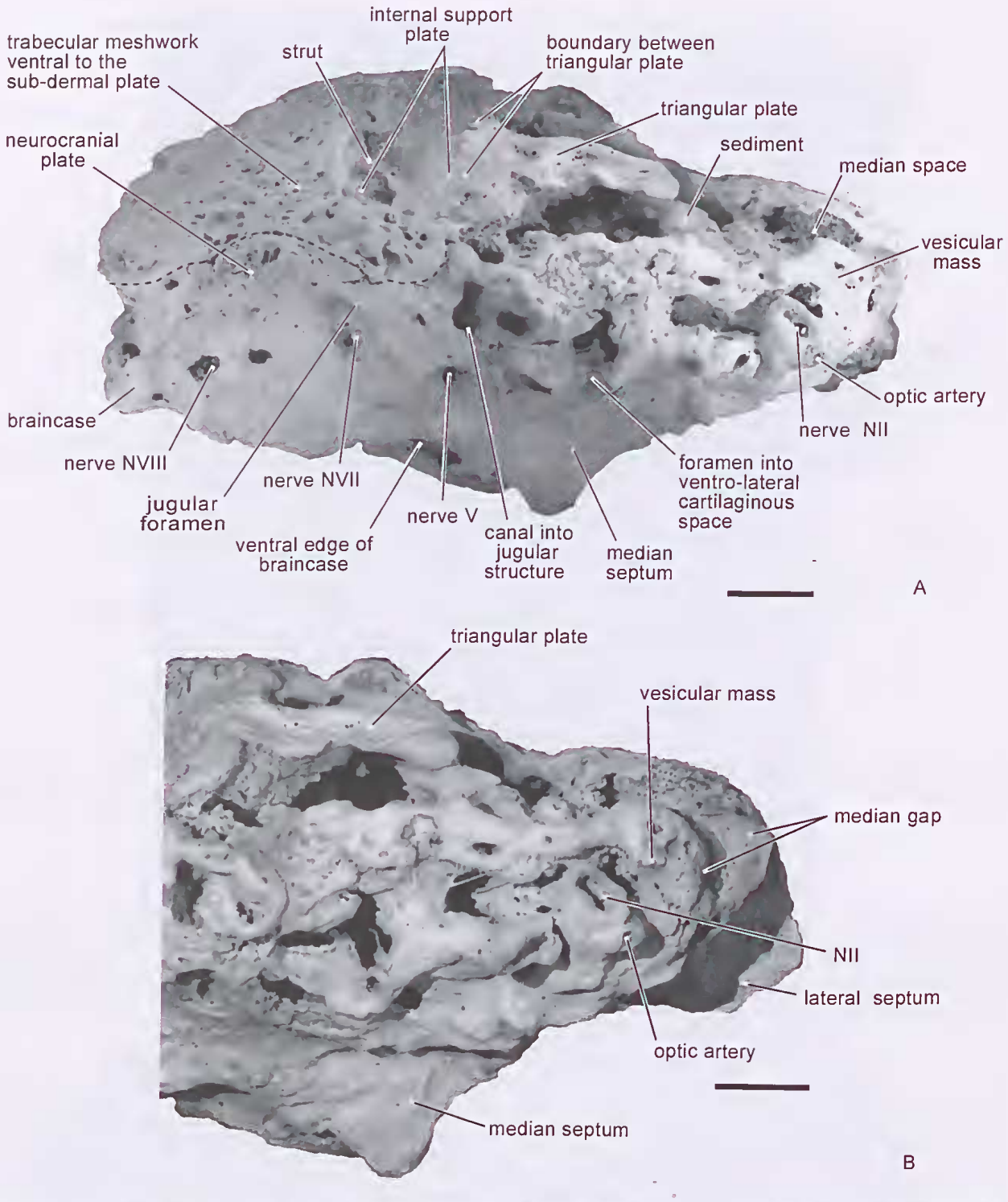


Figure 16. A. Right dorso-lateral view of whole specimen. Junction between the trabecular meshwork ventral to the sub-dermal plate and the neurocranium shown by the dotted line. B. Eroded anterior end of specimen. Note the photographic shading in the anterior part of the image tends to obscure the main structures. Scale = 10mm.

The Anterior and Median Neurocranial Walls: The left side of the specimen is better preserved than the eroded right side (Fig. 17). The anterior surface can be exposed in dorsal view, and the ventral surface has to be observed in lateral view. Both sides have been viewed by tomographic sections.

In the axis of the specimen, only part of the neurocranial wall has been preserved, but the relics show that the left and right neurocranial walls become confluent and form a solid median septum (Fig. 14; also tomographic on Figs 27–28). The median septum is cut away anteriorly in an arc. The septum is slightly deformed, and in this position it forms a small internasal cartilaginous septum. The posterior part of the median septum is eroded away, and the walls of the braincase are preserved near the posterior end of the specimen between the two sides of the neurocranial walls (Fig. 14).

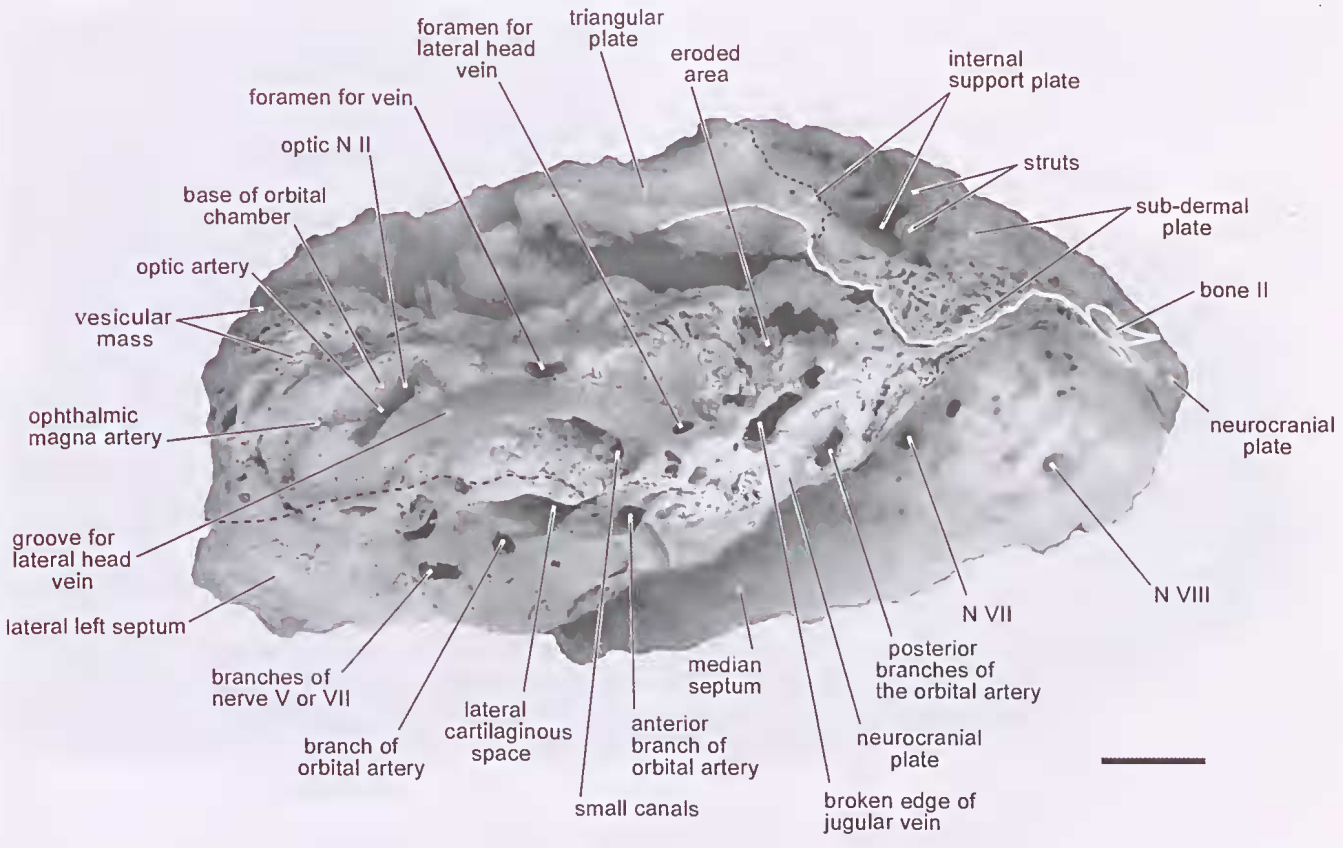


Figure 17. Slightly dorso-lateral, view of the left side of the specimen. (Anterior to the left.) The sharp boundary between the dorsal side and ventral side of the anterior section marked with a dotted line. Strong white line.marks boundary of dorsal plates. Bone II is just a small bone and its dorsal edge is concealed in the photograph. Scale = 10mm.

The preservation of the braincase is too poor to permit description.

Dorsal Anterior Walls of Neurocranium: The left side of the specimen is moderately well preserved. Entering the dorsal surface posteriorly is a large foramen (Figs 3, 14) that can be traced through an internal canal to the jugular foramen. Part of the eroded dorsal side of this canal can be seen on (Fig. 17). We regard this as carrying the jugular vein to the lateral head vein. As shown on Figure 26, the jugular vein runs into a foramen that opens on the exposed dorsal surface as for the Lateral Head Vein. This vein runs in a. groove that runs anteriorly leaving a clear passage for the vein that must have been covered with soft tissue in life. It is 3–4mm in diameter. The dominant feature on the dorsal surface is the groove for the lateral head vein and this runs to within 18mm of the edge of the specimen where it meets a slight ridge (Fig. 17).

Towards the end of the of the lateral head vein there is a deep cavity (Figs 17, 28A), within which there are two foramina. The posterior foramen is much larger and it runs poster-medially towards the braincase. Part of its internal course can be traced on Figure 28B, C. We interpret this as the optic nerve N II. The smaller anterior foramen carried the optic artery. We consider that the optic space occupied a large area that has been eroded. The base of the chamber still retains the groove for the ophthalmic magna artery (Figs 3, 17). Although the right side of the specimen was eroded, the position of the optic nerve N II is well preserved (Fig. 16). One difficulty with this interpretation is that the orbit is placed in a dorsal position, well forward from the nerve N V. The position of nerve N VI cannot be identified.

Another foramen on the median side of the groove for lateral head vein enters a canal that runs more or less ventrally into the median lateral cartilaginous space (Fig. 17). We consider that it probably contained a vein. Lateral to the foramen for the lateral head vein four small foramina that open into small canals (labelled small canals Fig. 17). These are connected with the foramina on the dorsal edge of the ventral side of the anterior surface as described in the next section of the text.

Ventral Side of the Anterior Surface: The ventral edge of the dorsal anterior face is sharp ridge, and is shown by a dotted line on Figures 17 and 18; and tomographically on Figure 27. Ventral to this ridge the surface drops into a slightly concave face. This is preserved on the left side of the specimen. The posterior part of this ventral surface is occupied by a large cavity that must have been filled with cartilage (Figs 18, 27B, C). The surrounding layer makes a complete tube (Fig. 18) that must have contained cartilage. We refer to this opening as the Lateral Cartilaginous Space, (and abbreviated to LCS). The median face of the cartilaginous surface would have continued anteriorly into a concave surface on the posterior part of the lateral septum. This concave space contains four grooves and these terminate in foramina that are the openings of canals in the interior structures (Fig. 18). The complex pattern of these grooves will now be considered in detail.

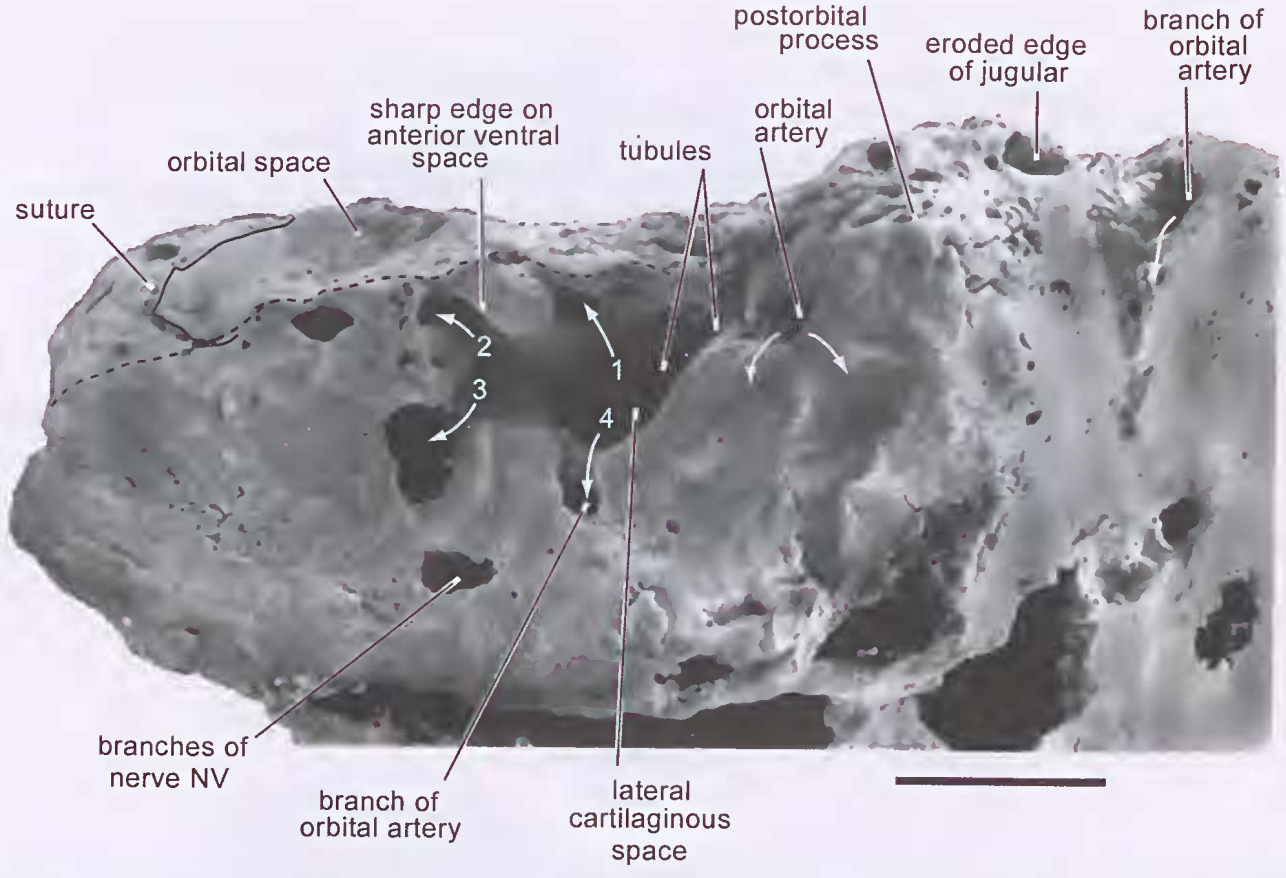


Figure 18. Ventro-lateral view of antero-lateral part of the specimen. Boundaries between dorsal and ventral faces shown by a dotted dark line. Details of connections between foramina and internal structures outlined in the text. Lateral extension of neurocranium is a rough rounded mass. Position of canals running from the anterior groove from the lateral cartilaginous space, are shown by white arrows numbered 1–4. Scale = 10mm.

The two dorsal grooves, labelled as 1 and 2 (Figs 18, 27C, 28A) bend postero-dorsally, and run in canals towards the lateral head vein. They connect with small foramina that open on the outer side of the lateral head vein. Dorsal foramen 2 also has a small canal that runs anteriorly, and it then passes into another foramen labelled as branches from dorsal foramen 2 on Figure 27C. This presumably acts as an exit of a vascular structure, but it also has a small anterior canal that runs internally but its course cannot be traced. The anterior foramen labelled 3 on Figures 18 and 27C issues into two main canals. The dorsal one is large and runs postero-dorsally towards foramen 1, but fracturing of the canal makes it impossible to trace its course. The ventral foramen in the same foramen opens into a canal that has been destroyed. The ventral branch 4 is very short, and although the canal leading from it is broken, a light shining down it shows that it merges into the side wall of the Lateral Cartilaginous Space (LCS). We consider that it carried a branch of the orbital artery (Figs 18, 27C).

The most ventral canal on the ventro-lateral surface opens through a foramen that internally connects with a canal that bends posteriorly sharply and runs posteriorly till it joins with the canal containing nerve N V_2. It contains the nerve ramus ophthalmicus superficialis, N VII, and its position is shown on Figure 23.

The Internal Structure of the Lateral Cartilaginous Space (LCS): The internal structure is lined with perichondral material that is poorly preserved. However enough remains to distinguish the following features. Postero-dorsally is a cavity that seems to open into the floor of the Centro-Lateral cartilaginous Space. It probably contains a branch of the jugular vein. Just ventral to this opening is a small rounded foramen joining a short canal running posteriorly. Its course could not be determined, but it is appropriately placed to carry a branch of the orbital artery. And finally there is another foramen described above as connecting with the canal 4 on the ventral face of the lateral septum. Summarily, we consider that the LCS carried extensions of the jugular vein and the orbital artery into the soft tissue occupying the lateral face of the head. Obviously, this soft tissue has been lost during preservation.

Centro-Lateral Cartilaginous Space (CLCS): This is partly preserved on the left side, but was eroded on the right side of the specimen. The perichondral surface is very poorly preserved, but Figure 19 shows the relics. The posterior wall is well preserved. It is entered by a foramen from the dorsal side (single black arrow in Figs 19A, B), but the canal is broken off prior to its entry. We consider that it must have been derived from the jugular vein that sends a canal to this region. Running ventrally from this foramen is a broad shallow groove that drops suddenly as shown by two posteriorly directed black arrows in Figures 19A, B. The lateral face forms a surface that rises to join the more dorsal skeleton, and more

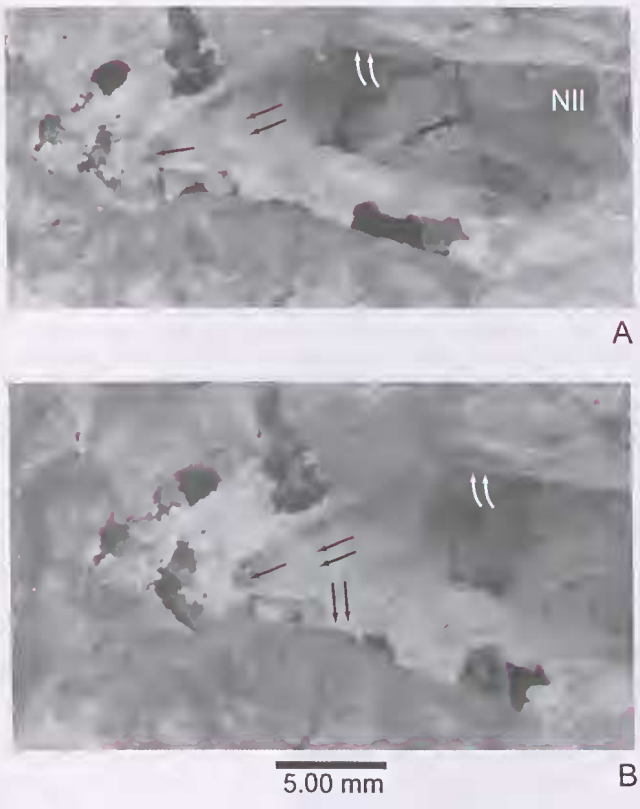


Figure 19. Two photographic views into the posterior cavity containing the centro-lateral cartilaginous space. Anterior of specimen to the right side. Much of the space is excluded by the lateral walls. A. Shows the posterior wall with the posterior foramina with a single black arrow, a furrow standing steeply with two black arrows indicating rapid descent to the broken up floor of the cavity. The deep lateral cavity running towards the lateral cartilaginous cavity is marled with two white arrows, and a single anterior black arrow runs into an anterior space. The approximate position of the canal carrying the nerve N II is marked. B. Anterior face tilted upwards, and the medial face is better exposed. Posterior face more clearly with the foramen with a single black arrow. A pouch running medially with two white arrows as on A. The two arrows medially directed mark a foramen. Some more details are mentioned in the text, but they could not be photographically illustrated because of the cover of the external bone. Scale = 5.00mm.

ventrally it turns laterally to form a pouch that runs into the Lateral Cartilaginous Space, shown by two white arrows in Figures 19A, B. Anterior to that pouch are some foramina whose function is not known.

On the median face of the groove beneath the triangular median dorsal plate, the fragment of the wall stands vertically, but it is broken off. Presumably it reached the edge of the triangular plate. It has a foramen that runs medially, but only the basal part remains (shown by two laterally directed black arrows in Figs 19A, B).

The ventral part of the CLCS is very complex, and it is partly destroyed as is shown on the Figure 19A. Near the point marked, the nerve N II enters the system and the passes to the braincase. The floor of this cavity runs ventrally beneath a transverse optic nerve N II, but its outline cannot be traced.

We conclude that the CLCS was a region within which the jugular veins diversified to serve the anterior parts of the specimens, and across which the optic nerve N II passes. Details of the distributions of the various elements require the discovery of better specimens.

The Palate

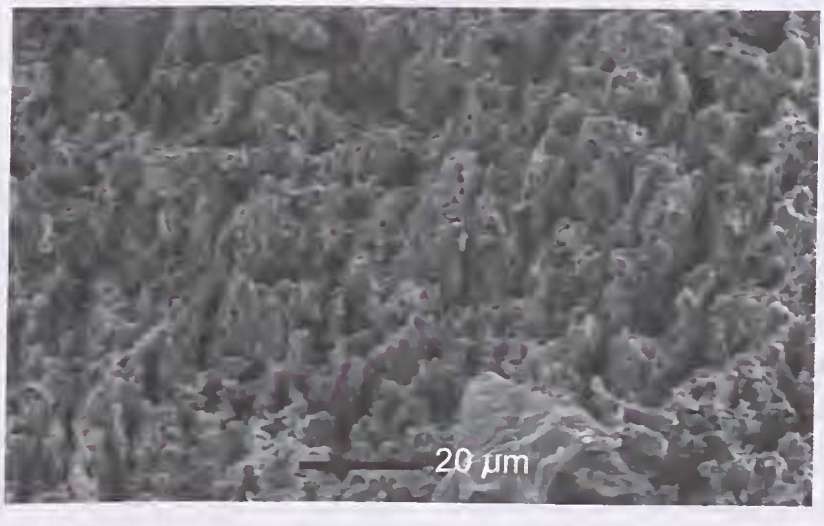
The specimen has no organised palate preserved. Several fragments of what may have been the broken up fragments of the palate were loose in the etched surface in tadly concave, and it is transversely finely ridged. Antero-medially a break continues across the roof and the unridged surface is more inclined dorsally (Figs 14, 21). Part of this surface has perforations similar to those in the overlying bone. Lateral to that the roof of the capsule reaches the broken edge of the specimen. We interpret that this surface approached the external nostril. The lateral edge of the capsule is bordered by the lateral position near the anterior end of the median septum. Each item consists of a small structure 2–3 mm across. The buccal surface of each unit has a number of irregular depressions on which there was no pattern of radial lines. The surface also has a number of small pits, and where they are worn away fine grooves are present running oblique to the surface (Fig. 20B). SEMs of the longitudinal surfaces show that the body of the structure is composed of parallel canals oriented in different directions (Fig. 20A). The mechanism by which these were deposited remains unknown.

Similar blocks of material have been described from *Cheirolepis trailli* (Pearson & Westoll 1979, Fig. 8), and each block has a radiation centre. Such centres are not present on our material. Unfortunately the internal structure of the *C. trailli* has not been described.

Exposed Anterior Face of the Specimen: The anterior end of the specimen was eroded and none of the rostral region is preserved. In dorsal and anterior views, the left side the residual material is well preserved, and it is made of vesicular bone separating multiple spaces. This is well shown in anterior drawing in Figure 21; and also on thick tomography sections in Figures 27A, B. A thick section is imaged by tomography (Figs 22A, B). These sections also show some sedimentary material that was not etched, and it is shown up on the image coloured in transparent green. Branching canals are present on both sides of the specimen, but they are not generally interconnected. There is no evidence that the canals carried nerve tissue such as those found in other osteichthyans where nerves N V and N VII are well known. On the exposed anterior of the eroded surface they appear as a number of ovate spaces that are separated by strong walls. This also supports the view that the tissue is not nerve carrying.

These structures are in contact with the dorsal side of the olfactory capsule. They could be considered as a support structure for the large olfactory capsule, but the size and complexity seems excessive for such a function. They may support the rostral region of the organism. The outer edge of this vesicular mass on the anatomical left side is marked by a suture that runs antero-laterally and separates the mass from the tissue that contains the optic nerve (Figs 3, 18). Details of the bone structure are illustrated on the tomographic sections.

A



B

Figure 20. Scanning electron microscope image of a fragment of what is interpreted as a piece of the broken up palate. (Details see text). A. Shows a lateral view with the surface in top left hand corner, and the linear arrangement of the tissue in different orientation. B. Dorsal view of the surface with the fine pores where the tubules shown in Fig. A meet the surface. Scales as shown.

Olfactory Capsule: A coloured image of the olfactory capsule supported by the trabecular bone is shown on Figures 27A and B, and also the structure of the lateral septum. Although the preserved surface is larger than one would expect, the following points indicate why we have interpreted this structure in this way: (a) the slightly displaced olfactory nerve N I appears posteriorly in our interpretation along with a branch of nerve NV_2; (b) the position and branching of the perichondrial canals for NV_2 and N VII posterior to the surface, is what one would expect posterior to the olfactory capsule; and (c) the position of the braincase as determined from the orbital nerve N II, is appropriate.

The roof is concave, and it is transversely finely ridged. Antero-medially a break continues across the roof and the unridged surface is more inclined dorsally (Figs 14, 21). Part of this surface has perforations similar to those in the overlying bone. Lateral to that the roof of

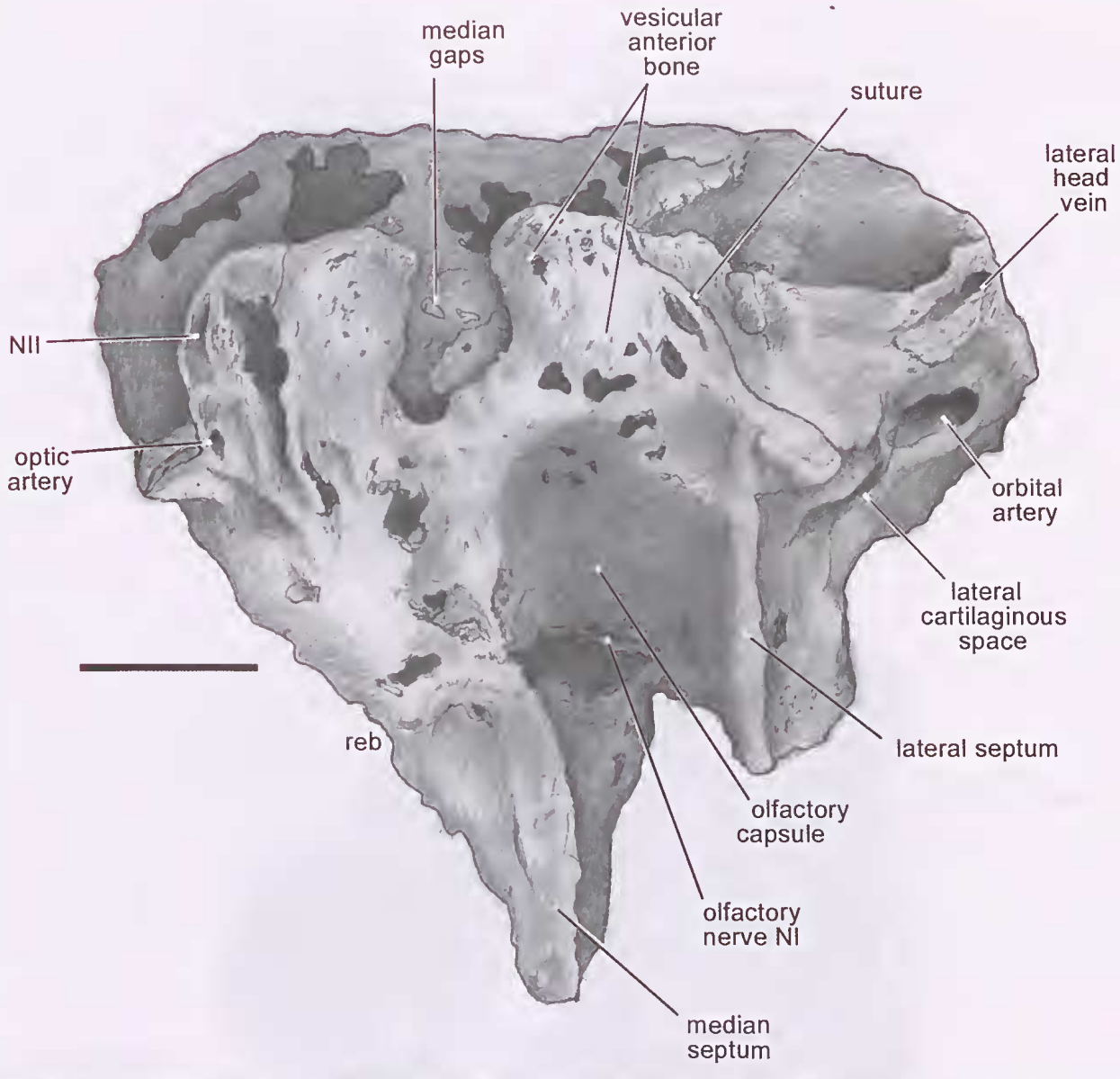


Figure 21. Drawing of the anterior view of whole specimen showing the highly eroded left side and the less eroded right side. Erosion has removed the right olfactory capsule. Anterior view of the left olfactory capsule with the end of the olfactory nerve at its posterior. Anterior end of the nasal capsule slightly eroded exposing the vesicular mass. Median septum is well posterior of the anterior edge of the specimen. Lateral cartilaginous space is compressed in this image. Compare with Figure 27 A, B. Scale = 10mm.

the capsule reaches the broken edge of the specimen. We interpret that this surface approached the external nostril. The lateral edge of the capsule is bordered by the lateral septum, and medially there is the relic of cartilaginous internasal ridge.

The position of the olfactory nerve N I is critical for this interpretation. The tubular skeleton posterior to the nasal cavity is broken away, and to save the structures their edge is attached by glue to the back of the capsule. The tubules are very delicate and slight movement will cause them to be disrupted. A small amount of distortion has occurred, and in the following we have allowed for this. A large canal is preserved entering the olfactory chamber from a postero-dorsal (probably a posterior direction before distortion Figs 14, 23). This canal runs posteriorly for about 1 cm runs toward the braincase, and although partly broken off, its extension is visible. We interpret this as carrying the olfactory nerve N I (Figs 14, 23).

Adjacent to the olfactory canal is a somewhat narrower perichondral canal, and it runs postero-dorsally for *ca.*1.5 cm from its separation from the canal carrying the olfactory nerve. Clearly it enters into the olfactory capsule, a feature of the nerve maxillaris N V_2.

Posteriorly this N V_2 branch joins a second branch that runs dorso-laterally to a point just posterior to the olfactory capsule. There it turns sharply laterally and opens through the wall of the lateral septum. This nerve must have served the antero-lateral parts of the rostral region, and we interpret it as carrying a branch of the ophthalmicus superficialis N VII. At the very posterior end of the system where these canals join they make a single unit that is broken across. The junction with other structures is lost. We assume that it runs anteriorly from both the facialis and the profundus nerves as sometimes occurs in holodipterans.

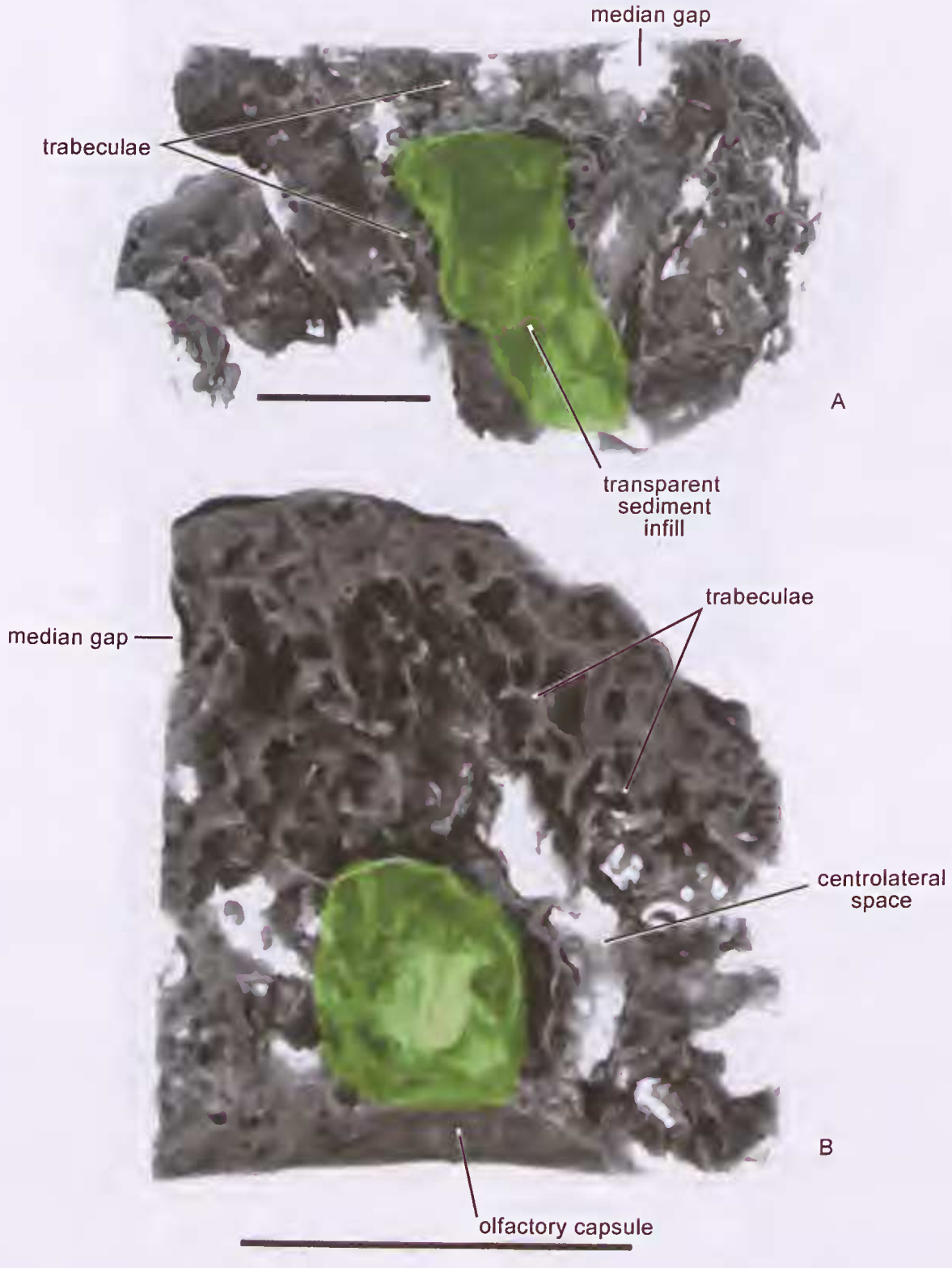


Figure 22. Tomographic sections through the anterior part of the specimen. Sediment remains transparently coloured in the axial regions, and their boundaries shown by hard lines. A. The right side of the image has irregular patterns of trabeculae without tubules. B. Right anterior transverse tomographic section through the morphological right side of the specimen, crest of the olfactory capsule ventrally, and median gap laterally. Trabeculae do not show signs of formation of canals. Large gap in trabeculae on right side of image are openings into the centro-lateral cartilaginous space. Scale = 10mm.

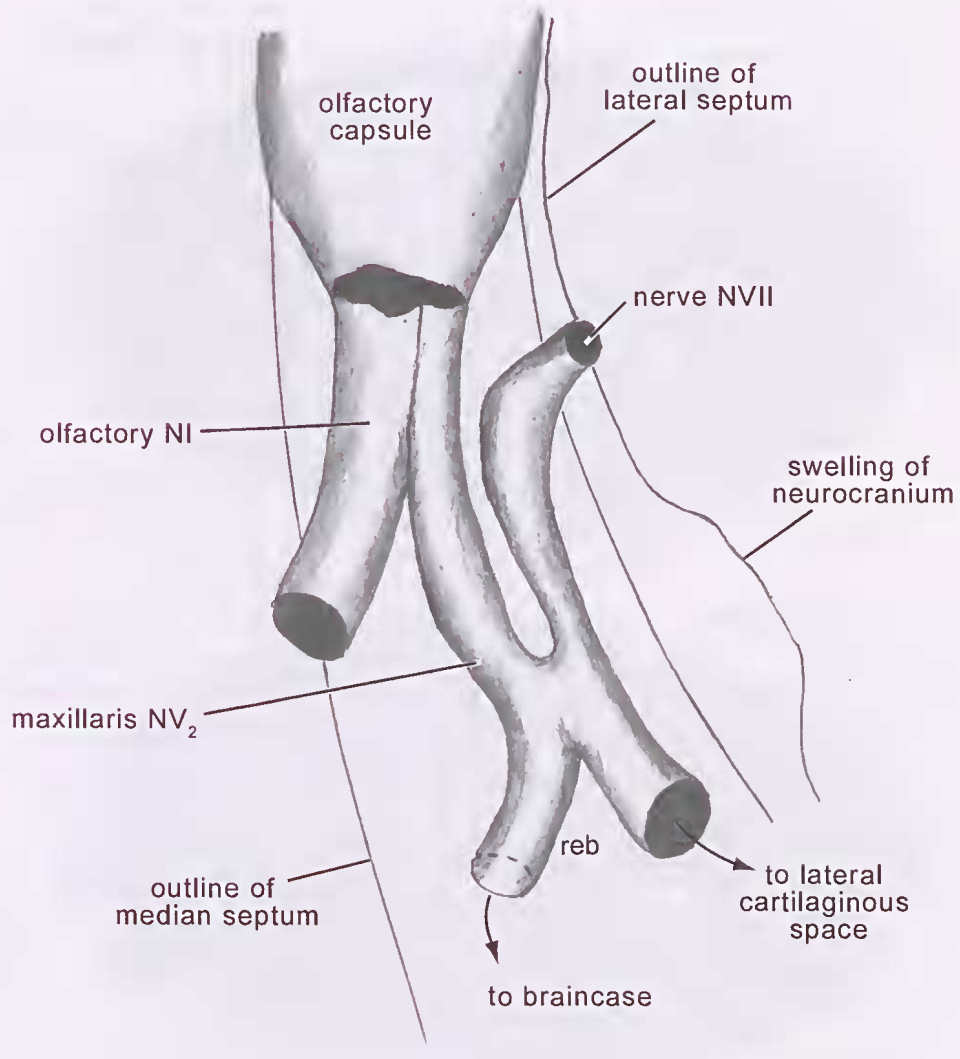


Figure 23. Reconstruction of the pattern of the nervous system posterior to the olfactory capsule. The system is very delicate and has been slightly moved from its original position. Interpretation is given in the text. Scale = 10mm.

Relationships

The relationships of this organism can be tested against a number of critical points. For this reason we consider the each major group as a separate item.

The total format, including the absence of a platybasic skull, and the position of the orbits, and the structure of the jugular drainage system, all indicate that this specimen is not an Agnathan (Wang 1991; Forey & Janvier 1994; Janvier 1996).

Among the gnathostomes, it has strong bony structures not found in chondrichthyans. The remains of the skull roof with the elongate sub-dermal plate may be suggestive of a placoderm arrangement, and the arrangement of the nerve N VIII and the lack of a labyrinth cavity attached to the margins of the braincase, and the anterodorsal position of the orbits are suggestive of a placoderm relationship. (Young 1979, 1986). However the absence of an internal plate beneath the sub-dermal bones, and the arrangement of the endocranium suggest that the similarities are the result of convergence.

The suggestion that it may be related to the acanthodians seems to be contradicted by the size and strength of the undivided dorsal sub-dermal plate and its extension to the midline, the presence of an internal support plate, the length and strength of the median septum, the size and position of the jugular veins and the lateral head vein and the structure and position of the supraorbital plates. It has been suggested that the scales of acanthodians have an epidermally deposited sequence of layers and no dentine internally. This similarity is due to convergence. Consequently we are left with the Osteichthyians.

The fine surface structure of the supraorbital bones are unlike any actinopterygians from the Middle to

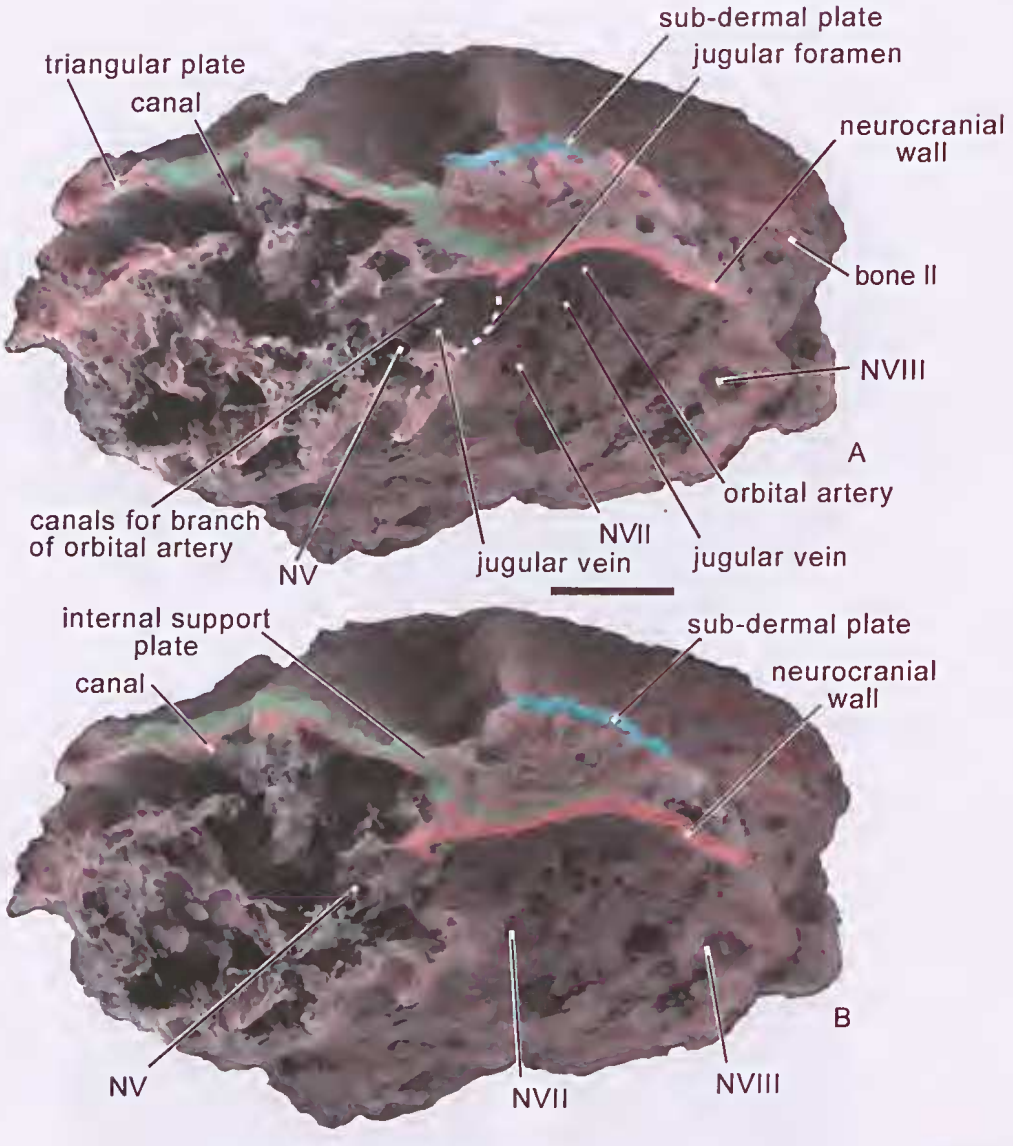


Figure 24. A. B. Two thick tomographic images of sections from the posterior part of the specimen. A. Is the more lateral section, with the opening for the jugular foramen outlined in a white dotted line. Images of nerves N VII and NV as they pass towards the braincase. The sub-dermal plate varies in thickness because of weathering. Sub-dermal plate coloured blue; internal support plate green; neurocranial wall red. Space between the sub-dermal and internal support plate filled with trabecular meshwork. B. More median slice with the positions of nerves N VIII, N VII and N V with clear. Scale = 10mm

Late Palaeozoic (Pearson & Westoll 1979; Reif 1982 p.314; Gardiner 1984; Basden & Young 2001; Long *et al.* 2008). Our specimen has distinctive bone structure, and surface rounded bosses that have no ganoin, and they are composed of sheets of material that have been deposited not (our emphasis) from dentine-like structures, but from the epidermis. None of these features is found in actinopterygians. Other significant features include the large median septum formed from the neurocranial wall; the large lateral septum connecting with the neurocranial wall and running laterally to the nasal capsule; the sub-dermal plate ventral to the dermal roof and also forming the outline on which the dorsal dermal plates were formed; and the large cartilaginous spaces in the median and lateral positions. In summary it appears that no unambiguous characters indicate an actinopterygian affinity.

So what of the sarcopterygians? The solid neurocranial walls are similar to some sarcopterygian patterns. The absence of an intracranial joint indicates that it is not a member of the Osteolepiforms, Rhizodontiforms, Actinistia, Panderichthyida or the Onychodontiforms, but such a feature is found in the Dipnoi. Although no tooth plates are present in our specimen, the structure of the median septum, the lateral septum, the large nasal capsule, the arrangement of the jugulars, the orientation of the remaining dermal bones, and the large cartilaginous spaces, indicate that it is not a dipnoan. The same may be said of the complex of bone ventral to the posterior sub-dermal bone and the structure of the internal support plate. The bosses on supraorbital bones and its surrounding bones are distinctive, and they are unlike the cosmine structure of the Devonian dipnoans. Clearly our organism is not a member of a sarcopterygian

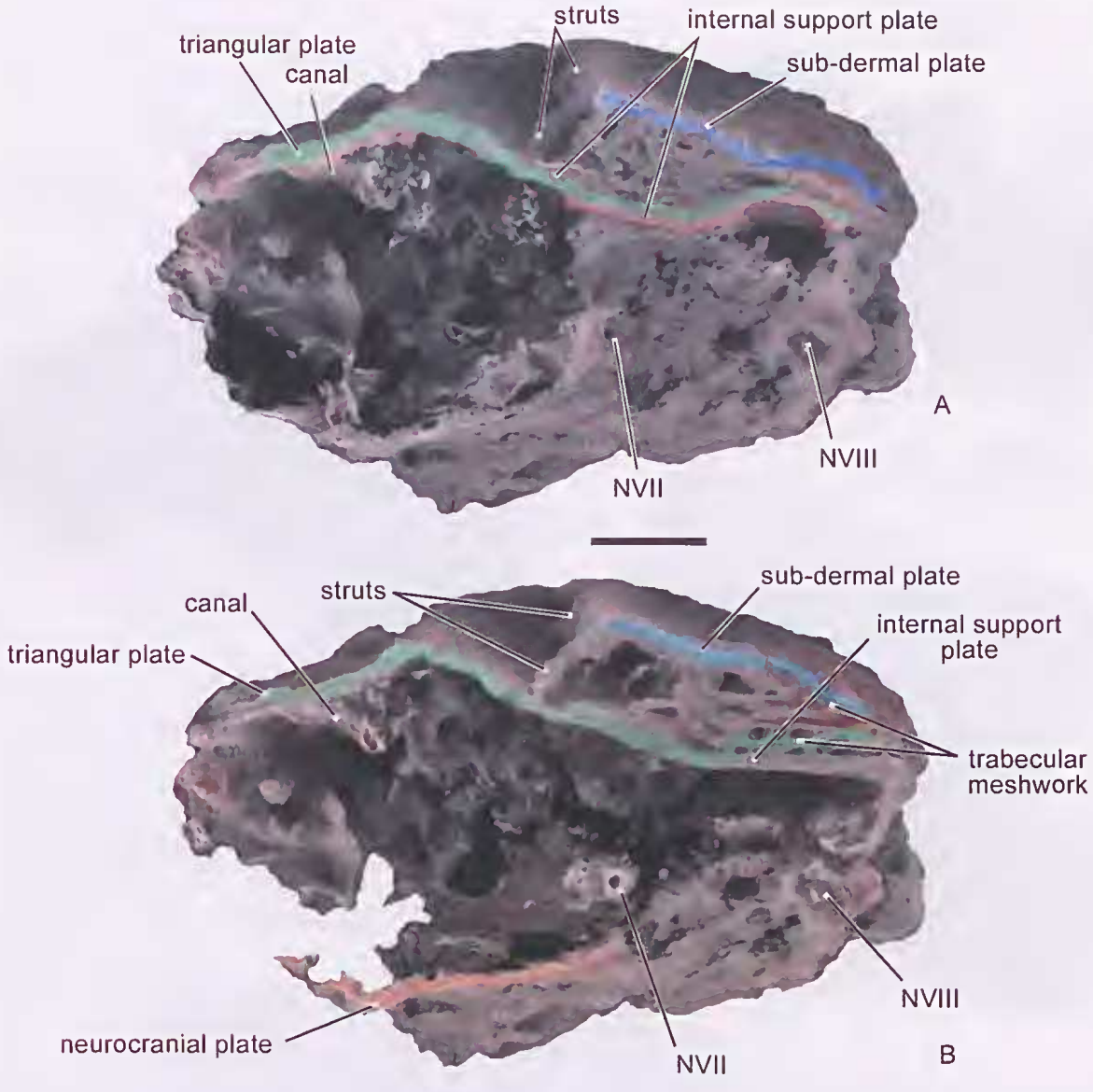


Figure 25. A. B. Two tomographic images cutting more deeply toward the braincase. and completing the series shown in Figure 24. Posterior to the struts the trabecular meshwork decreases in size indicating that the trabecular meshwork is strongest laterally. A. The section passes through the jugular foramen, and the nerve N VIII observed. posteriorly. B. The section is more median than in section A. The trabecular meshwork ventral to the sub-dermal plate is weaker medially in B than in A, indicating that the meshwork is stronger laterally. The presence of nerve N VII, and the canal from the triangular plate opening into a canal, are well outlined. Scale as in Fig. 24.

group as the subdivisions of that group are at present understood.

Despite this conclusion, we consider that the specimen indicates a new design of organisms, and should be placed ultimately in a new higher taxonomic status. In the absence of the dermal pattern of bones, the absence of a palate, and the lack of a mandible, it is impossible to establish such a higher taxon. This will await the discovery of more specimens. What then is the point of describing such an incomplete specimen as some reviewers have suggested?

Significance of discovery

Earth scientists naturally turn to environmental factors in attempting to understand the bases of major biological disparity and diversity. These usually consider such points as the abundance of oxygen in both the atmosphere and the oceans, the appearance of glaciation, unsettling of the carbon cycle, or even movement of continental masses and the evolution of continental shelves. Although any biological change has to be accepted by the environment to be successful, the origin of the changes must depend on the possibility of major changes in the genome. Such changes must affect the genomic stability, and produce the possibility of several new designs that may have short or long term possibilities that restore stability. In what follows in this text we examine some of these possibilities

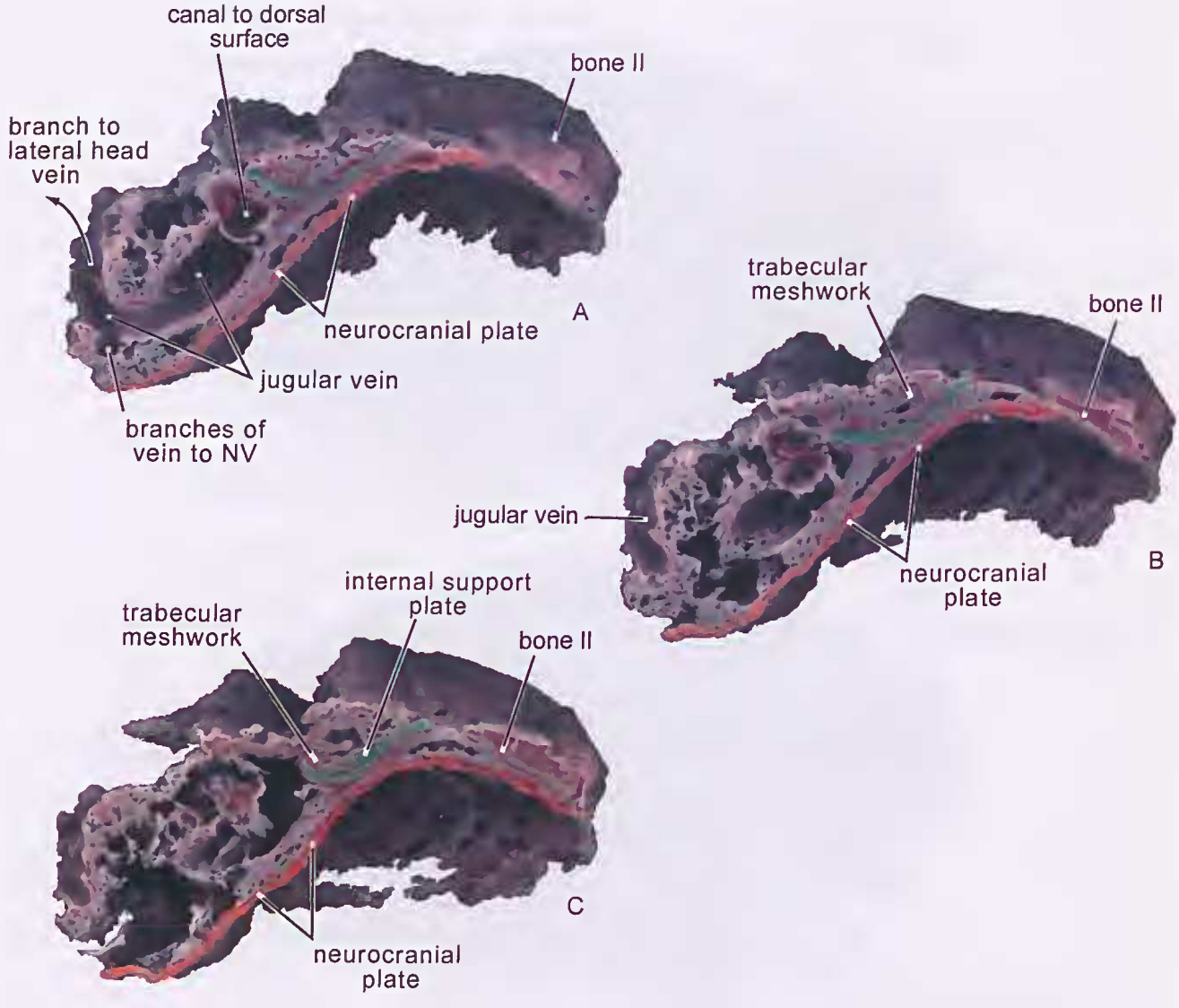


Figure 26. A. B & C. Three slightly oblique thick tomographic sections cut through the marginal part of the specimen, lateral to the jugular foramen and posteriorly through bone II. A. Has the anterior part of the jugular vein with its anterior end giving rise to a canal leading to the foramen for the lateral head vein. B and C. Two more sections cut more medially. The deeper the section the larger amount of trabecular meshwork displayed. Scale = 10mm

Most workers now accept that major changes in phenotypic patterns must take place by some process other than simple Darwinian speciation. One major process is the genomic regulatory systems, and this has been recently summarised by a geneticist Davidson (2001), in a major book on this subject. On page 13 of this work he refers to changes in patterns "to the developmental process by which special domains of unspecified cells are assigned 'regulatory states', thus ultimately creating fields of cells that will give rise to the diverse parts of a structure, an organ, an organism". A general review of the current situation is given by the geneticist Jones (2010) in an article that deals with biodiversity, natural selection and random change. We also point to the work of Carroll (2000) and Carroll *et al.* (2005).

Campbell & Barwick (2006) have discussed this point with the sarcopterygian group, Onychodontiformes, which evolved early in the Devonian and were extinct by the end of that same Period. The ancestors of this group, like those of the dipnoans, remain unknown. For discussion of the lack of ancestral groups see (Valentine 2006; Marshall & Valentine 2010). Further the importance of difficulties in identifying homologous characters in setting up cladistic analyses in attempting to understand the processes of deep evolution been discussed by Telford & Budd (2003).

Our attention to this process was first stimulated by the work of Miklos (1993) who attempted to understand what was happening with the first arrival of dipnoans in the Early Devonian. Despite extensive searching no dipnoans have been found in pre-Devonian rocks. In his first article on this subject, he sets out his main point in a summary where he commented that "The origin of body plans is the essence of metazoan evolution, **not** (our emphasis) the origin of species." Among many

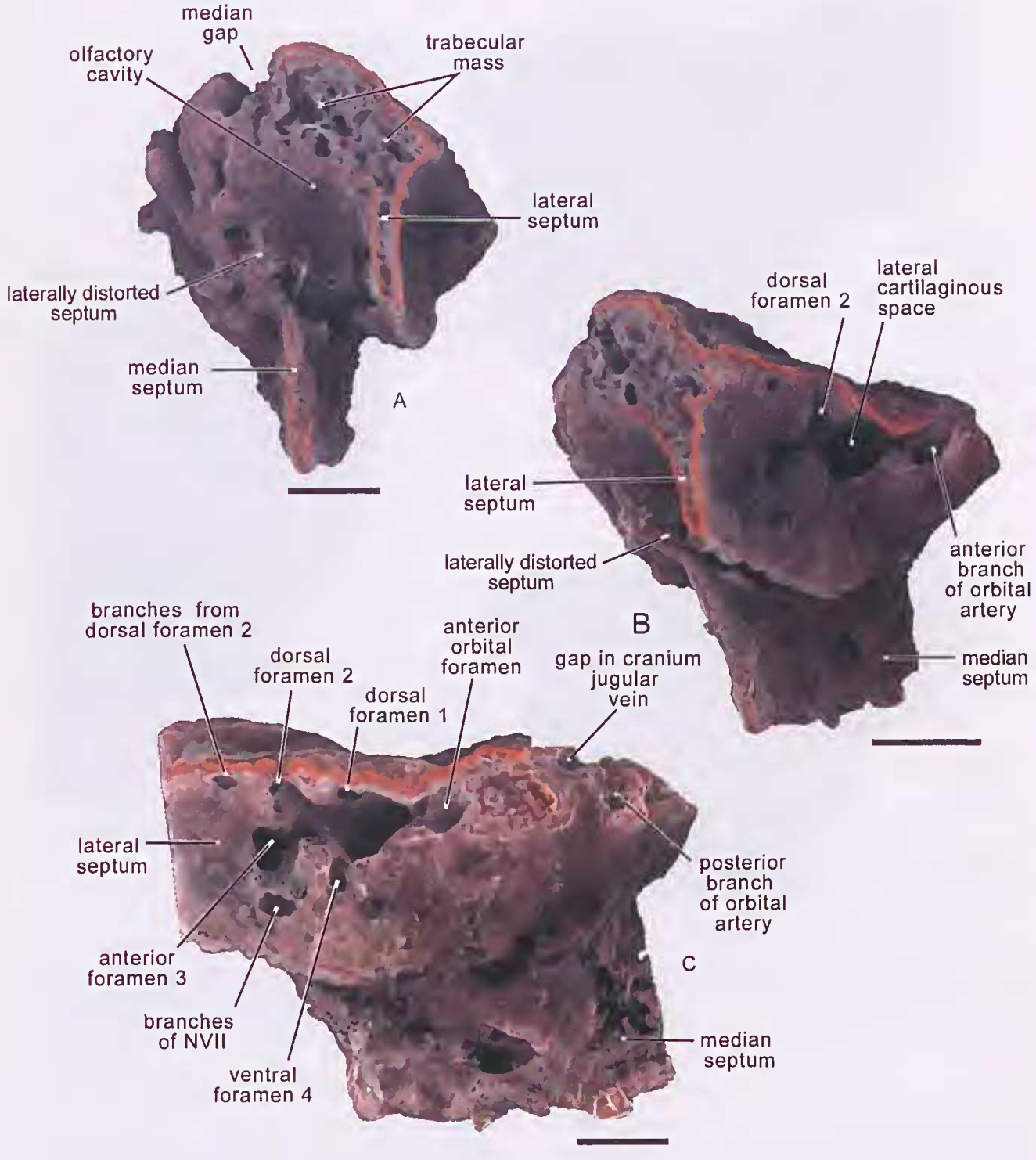


Figure 27. A–C Series of thick tomographic combination of sections. Sections through the neurocranial bones shown coloured red on all three figures. Ossified end of median septum situated posterior to the rest of the exposure. (Compare with Fig. 18). A. Is a section that cuts through the two septa. B. Sections from a more oblique view. The size of the lateral cartilaginous space is well shown, and it connects posteriorly into the anterior branch of the orbital artery. C. An even more oblique view including structures of the postorbital process with the posterior branch of the orbital artery as well as the ventral surface. (Compare with Fig. 18). Scale = 10mm.

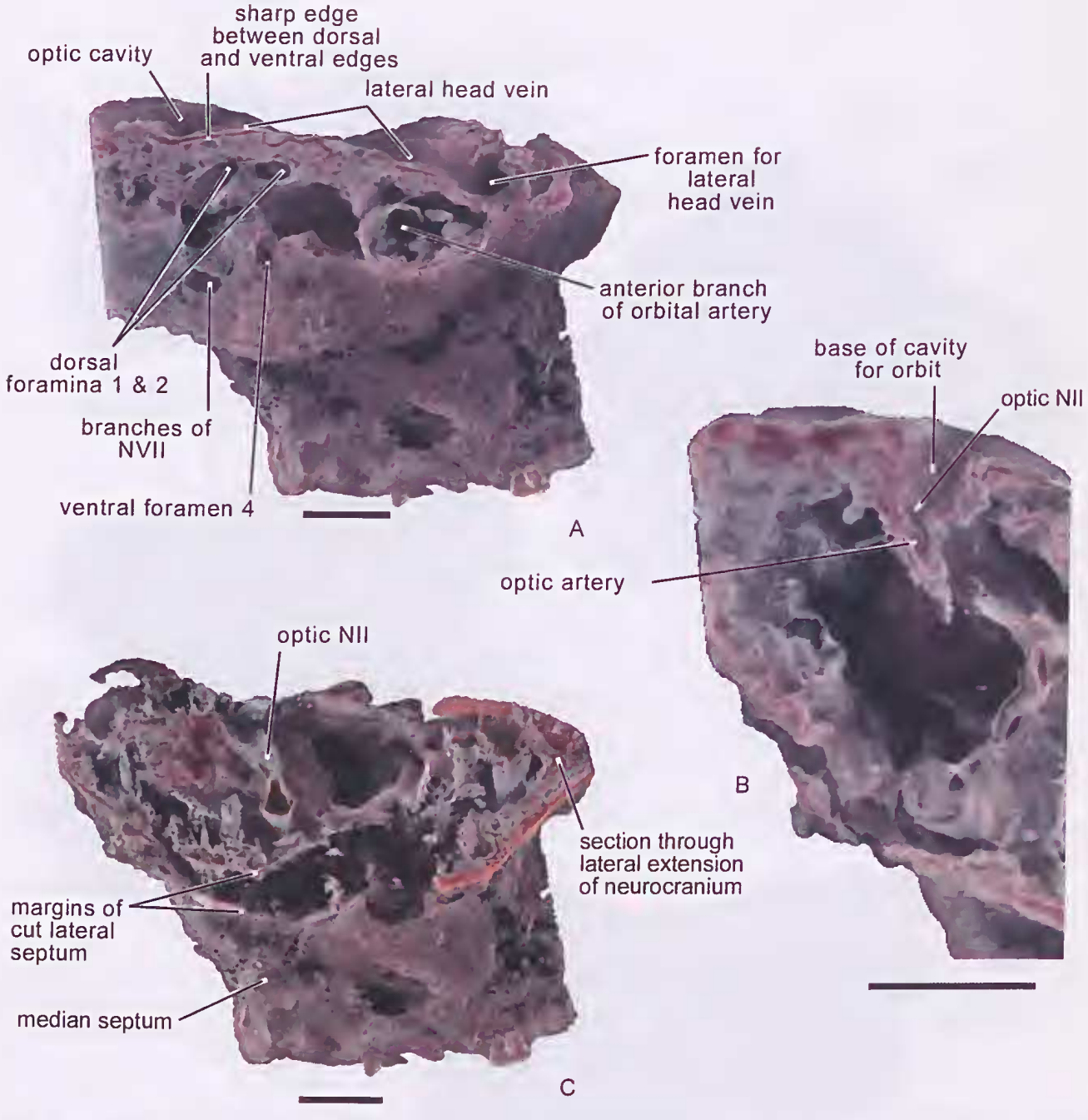


Figure 28. A. Thick tomographic combination of sections oriented to show the marked by edge of the anterior ventral surface. The edge of neurocranium coloured red. The position of the lateral head vein largely exposed dorsally along with the part of the optic cavity. Dorsal foramina 2 connected with the anterior foramen. (Compare with Fig. 18). B. An enlarged section through the base of the optic cavity with the canal for the optic artery and the base of the optic nerve N II. C. A much deeper oblique section that cuts through the lateral septum and shows the course of the optic nerve N II. Scales A–C = 10mm.

other significant comments he concluded that (p. 15) "little emphasis has been placed by evolutionists on the changes to the properties of regulatory elements in prokaryotes and eukaryotes, although there are some very thoughtful evaluations of this topic, including the enormous implications for development constraints ... it has not yet been modified to take into consideration the morphological changes that occur via the non-genic regulatory control regions in the genome." New genotypes will develop the possibility of new phenotypic patterns. A popular account of such phenotypic changes has recently been published by geneticist-ecologist, Bennett (2010), in which he refers to the chaotic course of evolution, and he points out that the non-linear pattern of macroevolution is vital. The use of cladistics in tracing macro-evolutionary patterns is really asking the wrong question.

The possibility of major changes in the phenotype is

now being explored from several points of view. Dover (1992) commented that "*De novo* combinations can spread under their own steam as a consequence of the instability of the genome". Among many other points Carroll *et al.* (2005, p.185) comments that ".... evolution of new regulatory lineages --- between signalling pathways and target genes, transcriptional regulators and structural genes, and so on --- has created new regulatory circuits that have shaped the development of myriad functionally important structures. These regulatory circuits also serve as the foundation of further diversification." Taft *et al.* (2007, p 297) in their discussion of the relationship between non-protein coding DNA and eukaryotic complexity, reached the conclusion that "non-protein-coding sequences that scale consistently with the developmental complexity, indicates that in addition to important innovations in proteins involved in developmental regulation and cell signalling, most of which were in place at the base of metazoan radiation, the expansion of the cis-and trans-acting regulatory architecture has been a critical factor at the evolution of the more developmentally complex organisms".

But it is not only regulatory changes in the DNA that are significant. Work on the RNA summarised by Dinger *et al.* (2008) has concluded that changes in RNA can produce changes in their function and the separation into protein-coding and non protein-coding RNA, and these are not readily distinguished. They also comment that "the very existence of such bifunctional RNAs challenges the assumption that the RNA world can be parsed between mutually exclusive protein-coding and non-coding categories." They end their conclusions with the statement that it is likely that "RNA is a molecular multi-tasker, whose roles can simultaneously bridge both the protein-coding and non-coding domains, and not only have more than one embedded function but also produce multiple products".

Along another line of approach, work by Stephen *et al.* (2008) on the highly conserved non-coding sequences, many of which are regulatory, appear with the development of tetrapods in the Late Devonian, our stratigraphic period of concern. The same article also concludes that the process of exaptation (Gould & Vbra 1982) is important in understanding the production of new genomic structures that do not produce immediate changes in the morphologic designs. Thus a genetic change may take place and be retained in the genotype but its phenotypic expression may take place later depending on the arrival of suitable condition for its expression (Marshall 1995; Shubin & Marshall 2000). If the conclusion of Taft *et al.* (2007) that most of the greatest major regulatory changes (for example the beginning of Phyla) were present at the beginning of metazoan radiation, one would expect that subsequent more minor changes would have been most abundant during the early and middle Palaeozoic. By that time most of the earlier changes would have established themselves, and subsequent changes would have expanded the organisms into the gaps after the older morphological changes at the phylum level took place.

This brings us to the point in the Early Devonian where major changes in the phenotypes of vertebrate phenotypes occurred. Not all the changes took place over a short geological time, and many of them left few descendants. But instability in the genomes did produce an explosion in sarcopterygians, where each of these groups produced a multiplicity of new types. For example, the dipnoans that first appeared in the Early Devonian, produced at least 30 new genera in the Devonian Period, and these included several new types of feeding mechanisms. In the later Palaeozoic many of these new types of feeding were lost, and the number of new designs was reduced, and with only one or two exceptions they used one type of grinding tooth plates inherited from the previous period. We consider that *Cainocara* represents perhaps a later example of the instability of the genome that produced the other osteolepiforms earlier in the Devonian.

The dating of the Gogo Formation is relatively secure. In terms of the conodont zones it is considered to be early Frasnian, well before the Frasnian/Famennian extinction. From our point of view the discovery of this new genus is an example of a distinctive phenotypic form that apparently occurs in a limited area. From the above discussion we consider that it arose by rapid modification of the genome making changes that were for a time produced exaptation. Similar morphological changes that were expressed all through the Devonian as conditions were appropriate for their expression.

Conclusion

Although this specimen is incomplete, we have enough material on which to conclude that it does not belong to any known described major systematic Order. Further searches in the field and in the laboratory have not found any other specimen that can be assigned to the same species. No evidence has been found of even traces of similar surface structures. This is a significant discovery in the light of recent work on the origin of new morphological designs that resulted from the genetic regulation.

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